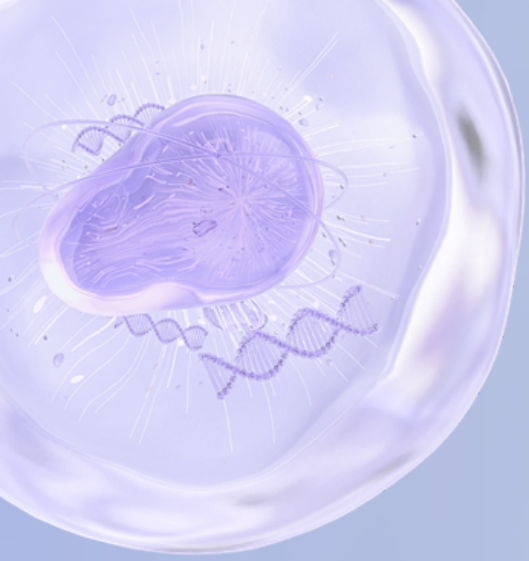




TOWARDS BETTER DECODING

READING DNA THROUGH PHYSICS

DIFA Summer School on Modeling and Data Analysis for Applied Physics
Bologna - June, 23th 2026

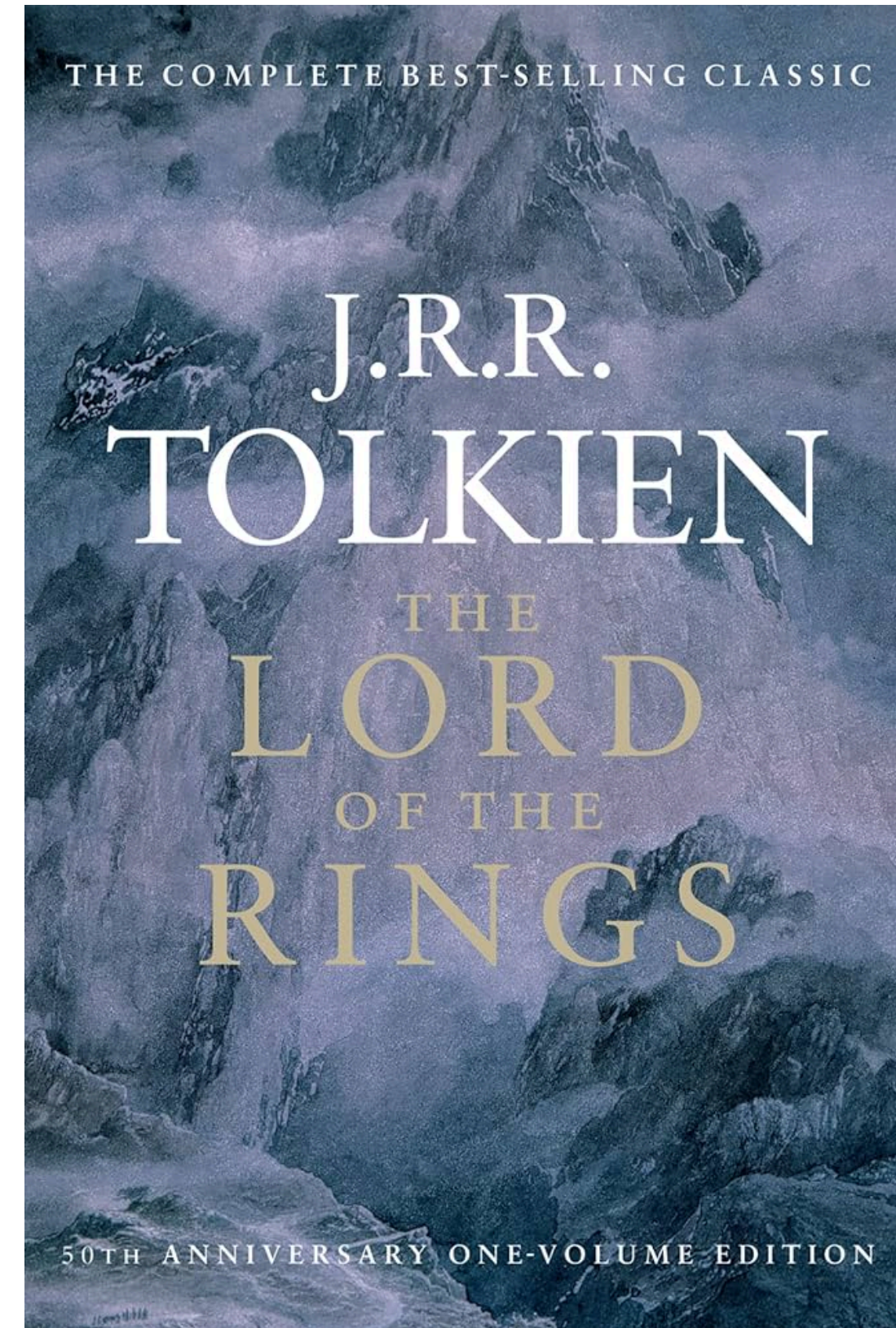


Francesco Casadei, PhD
Data Science and Bioinformatics Laboratory
IRCCS - Institute of Neurological Sciences of Bologna



The Lord of the Rings

How many of you
read this book?





The Lord of the Rings

Would you be able to reconstruct it
from text fragments?



Reconstructing a text

The part of chapter 1 I gave you: ~ **500**
characters

The entire book: ~ 2.5 millions (10^6) characters



Reconstructing the whole human genome

The whole human genome ~ 3.2 billions (10^9)
characters (bases)



Reconstructing the whole human genome

The whole human genome ~ 3.2 billions (10^9)
characters (bases)

How is it possible to reconstruct such a huge
sequence of characters?



DNA sequencing

What is?



DNA sequencing

What is?

How does it work?



DNA sequencing

What is?

How does it work?

Which techniques?



DNA sequencing

DNA sequencing is basically ‘reading’ the DNA of a subject (a human, a virus, etc)





DNA sequencing

DNA sequencing is basically **‘reading’ the DNA** of a subject (a human, a virus, etc)



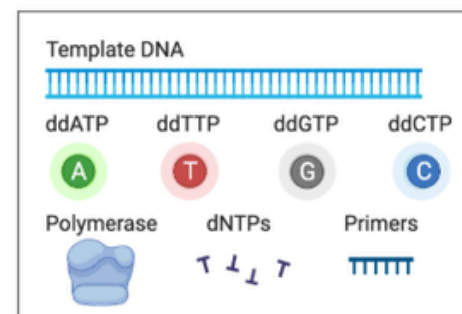
Not an easy task: we cannot use eyes or
microscopes



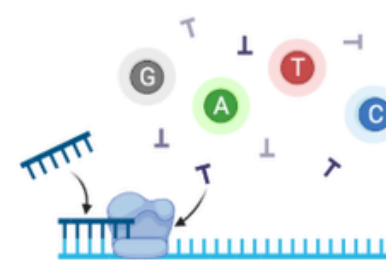
DNA sequencing

We need a workaround to recognize the different nucleotides

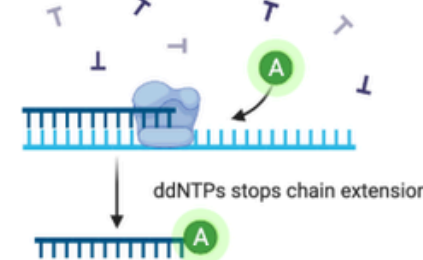
Reagents



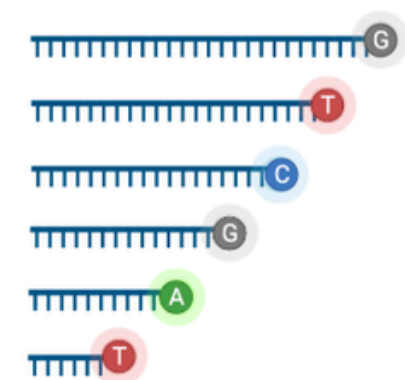
① Primer annealing and chain extension



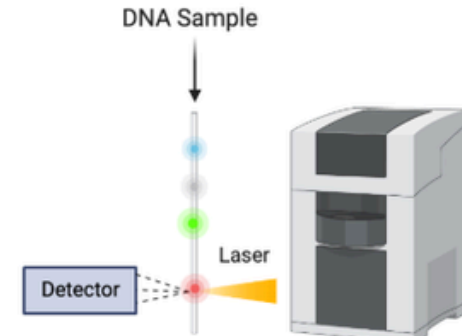
② ddNTP binding and chain termination



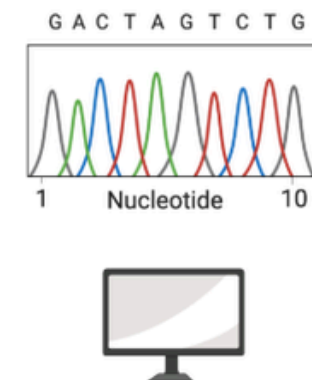
③ Fluorescently labelled DNA sample



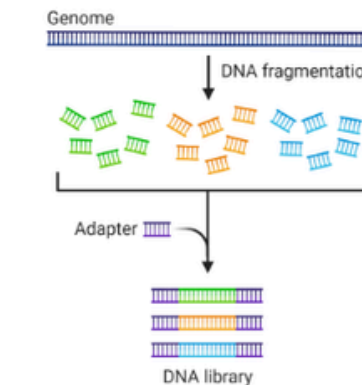
④ Capillary gel electrophoresis and fluorescence detection



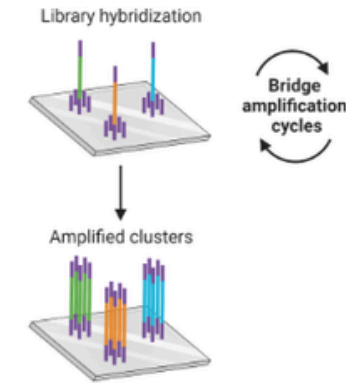
⑤ Sequence analysis and reconstruction



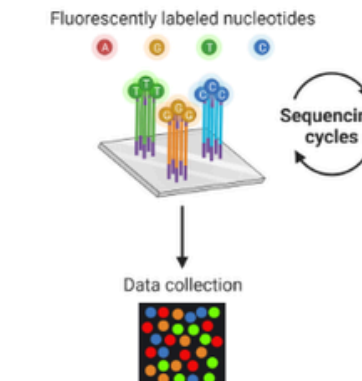
① Library preparation



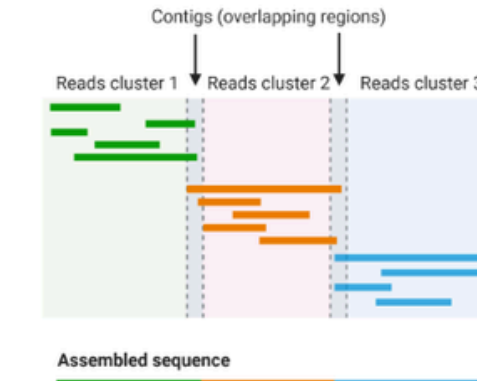
② DNA library bridge amplification

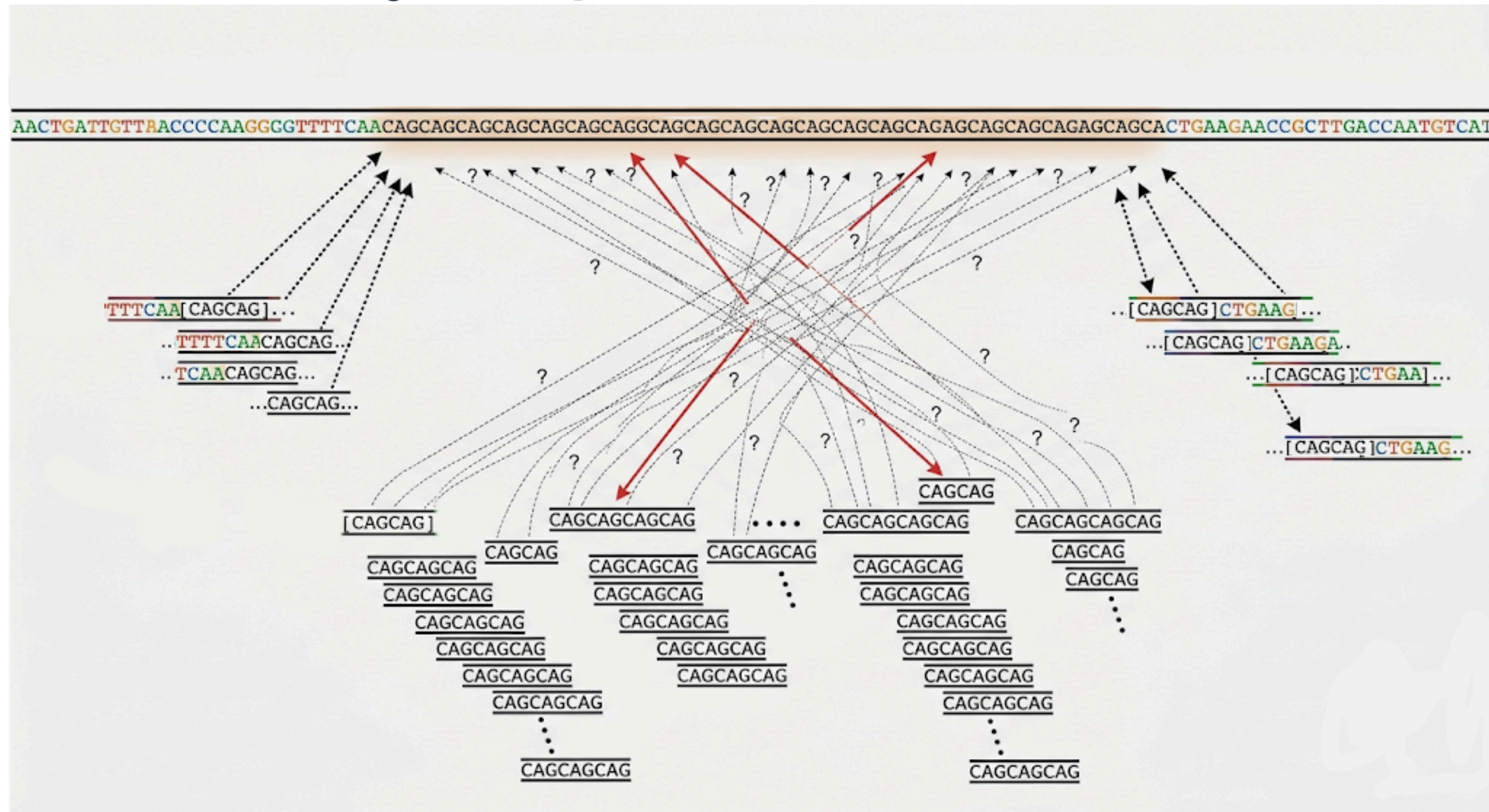


③ DNA library sequencing



④ Alignment and data analysis







DNA sequencing with physics

We would like to get longer reads

How?



DNA sequencing with physics

We would like to get longer reads

How?

Can we use **physics for DNA sequencing?**



Hypothesis I

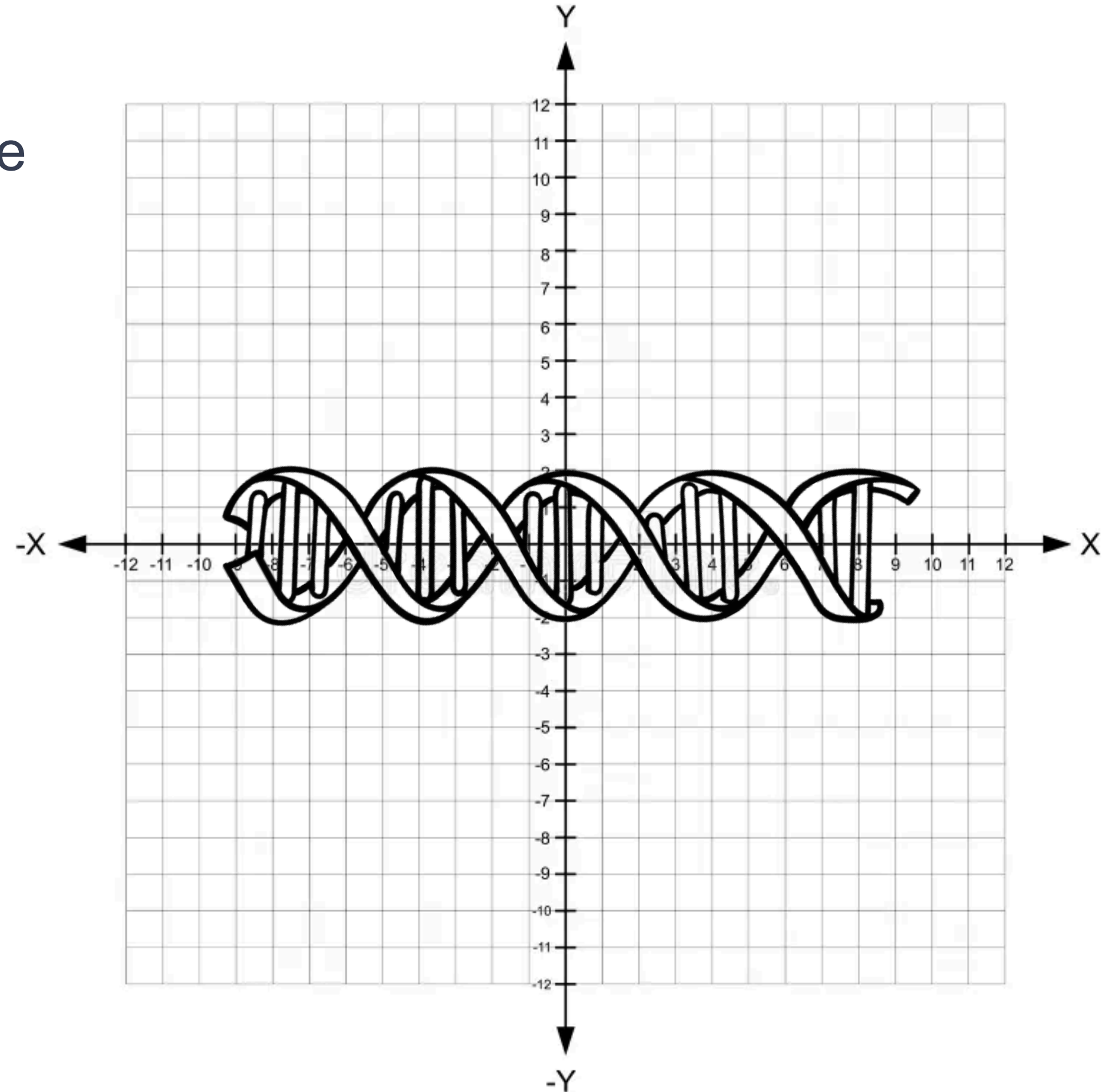
DNA has a periodic structure





Hypothesis I

DNA has a periodic structure

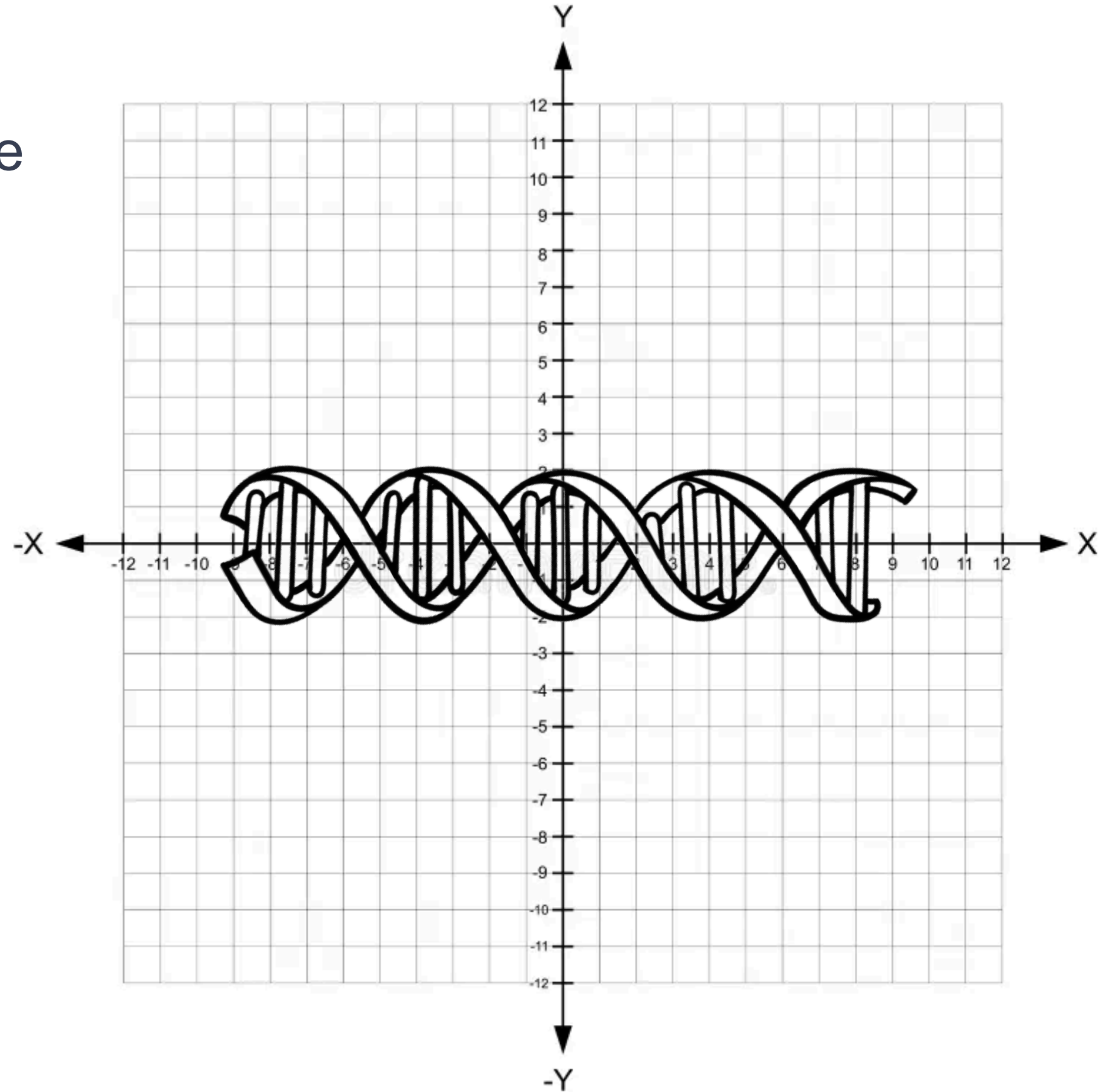




Hypothesis I

DNA has a periodic structure

$$m \frac{d^2 \vec{x}}{dt^2} + b \frac{d\vec{x}}{dt} + k\vec{x} = 0$$





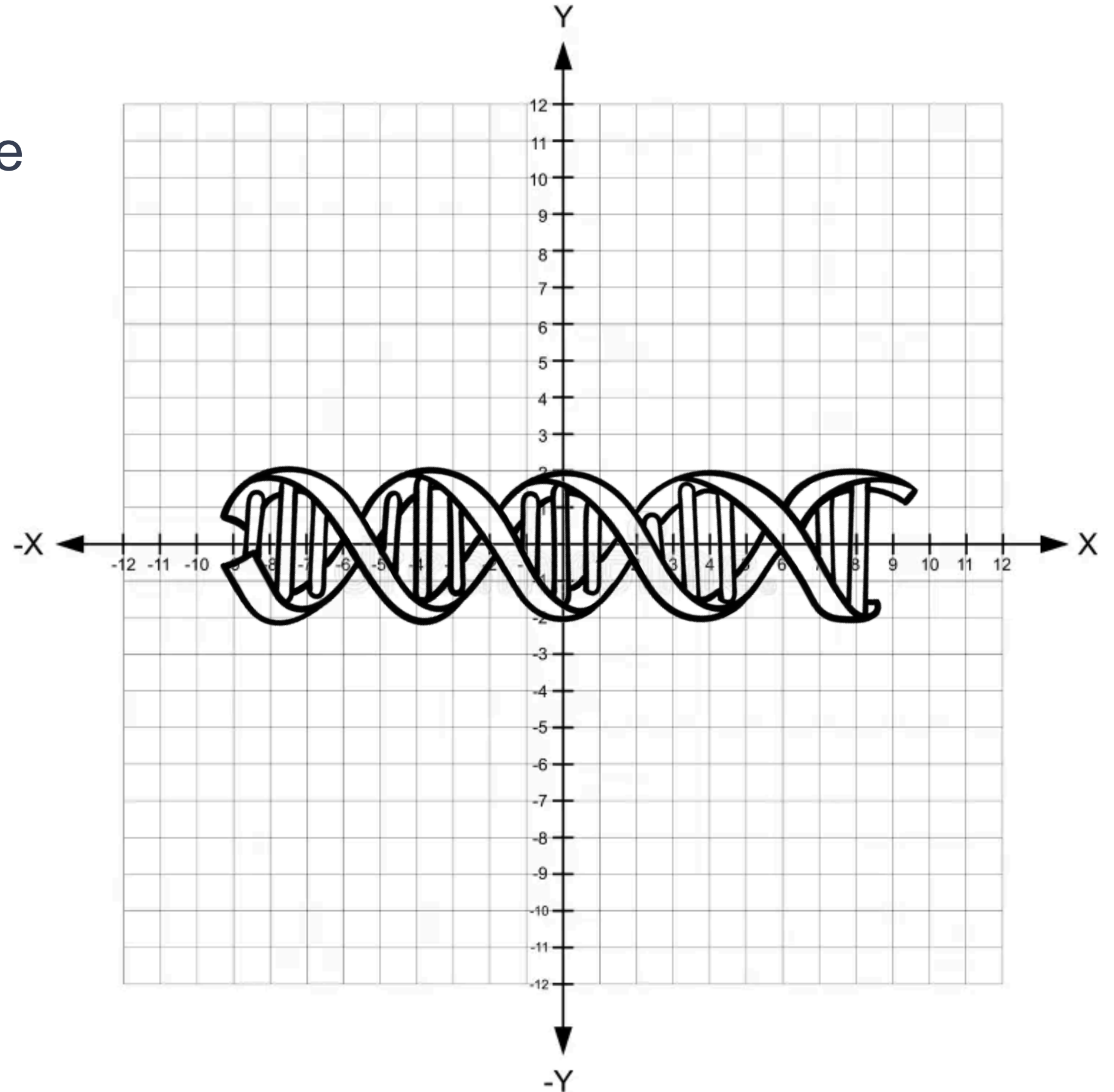
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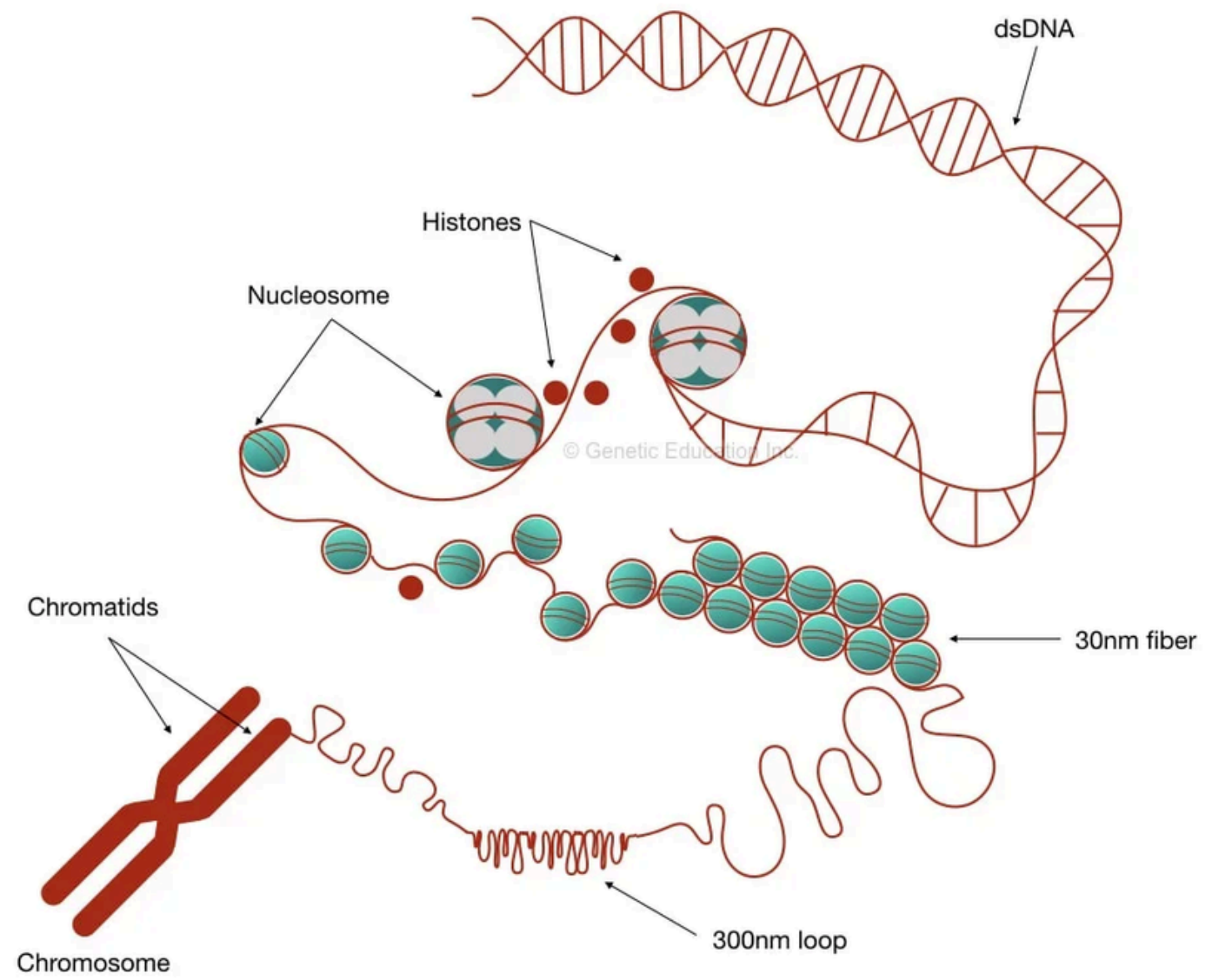


What about modeling it as a harmonic oscillator?



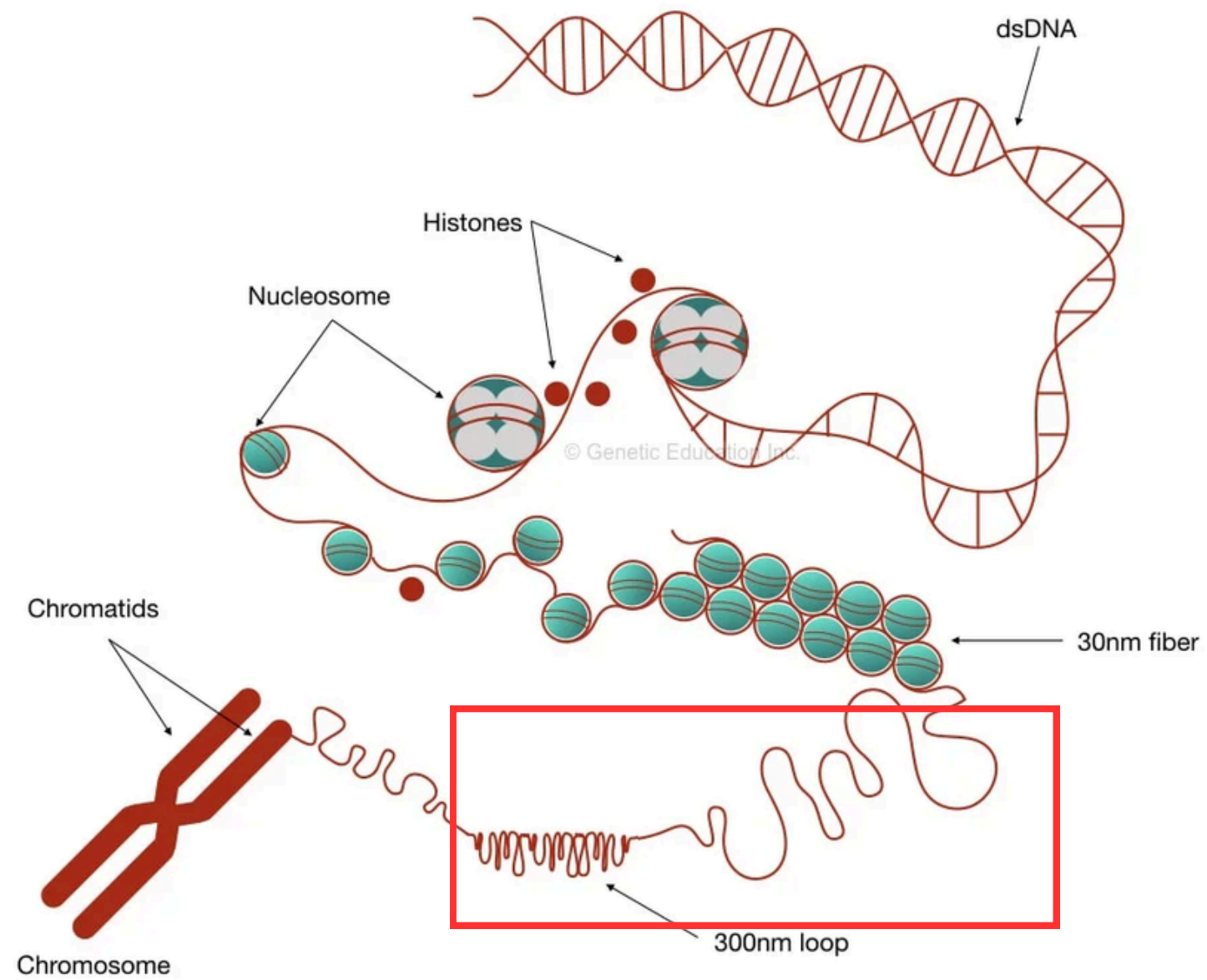


Hypothesis II



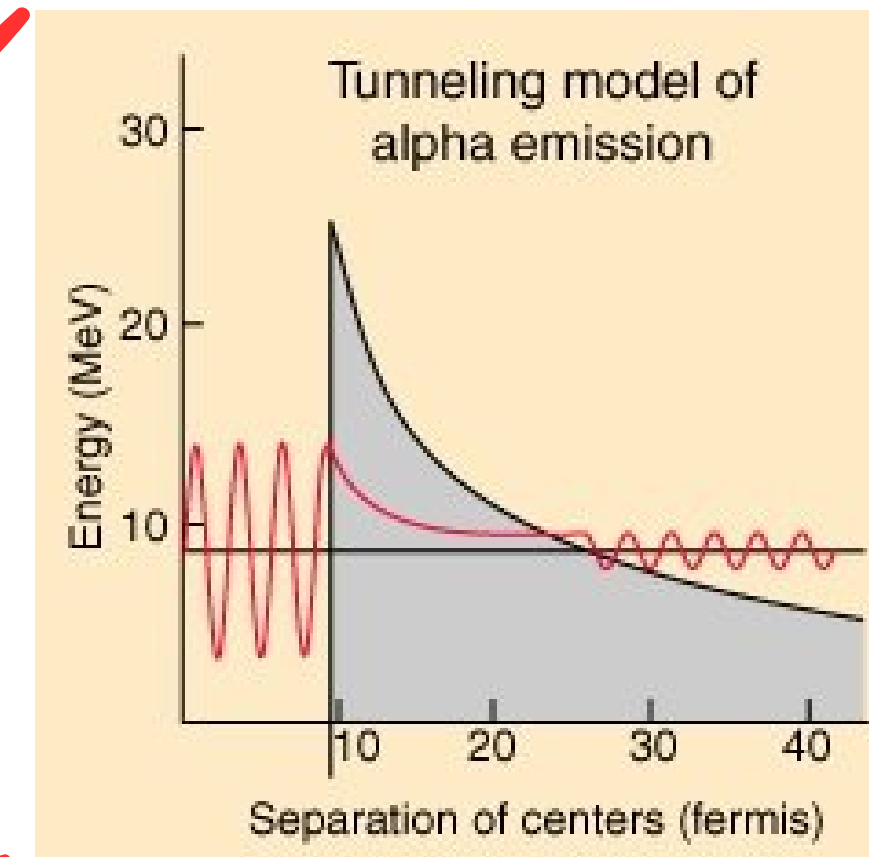
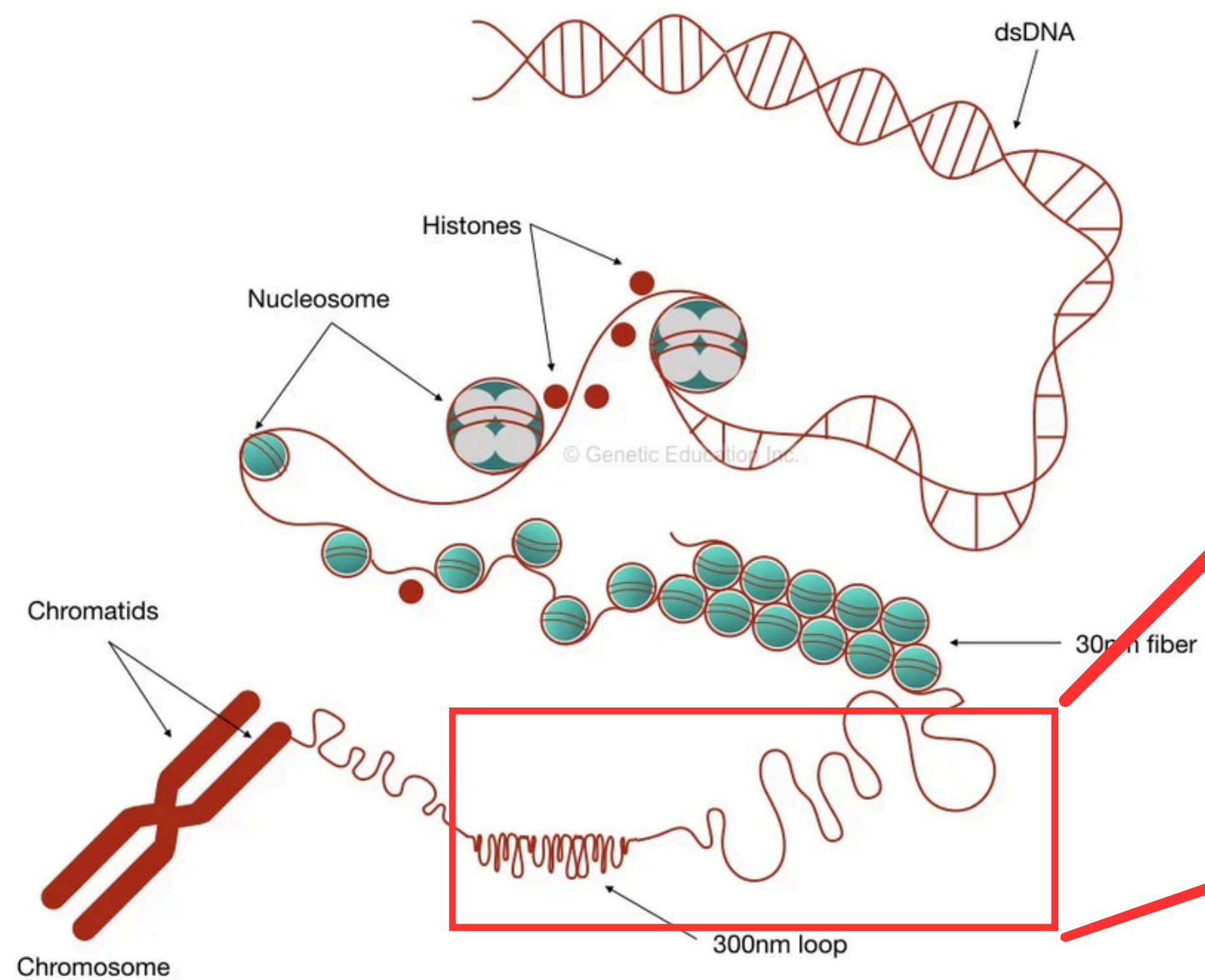


Hypothesis II



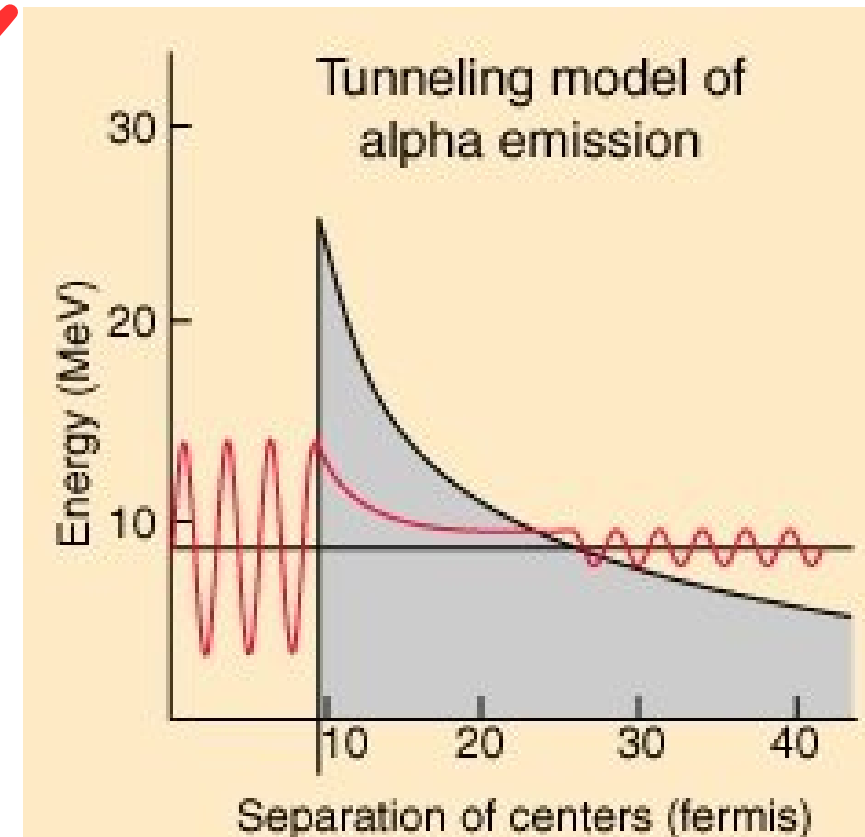
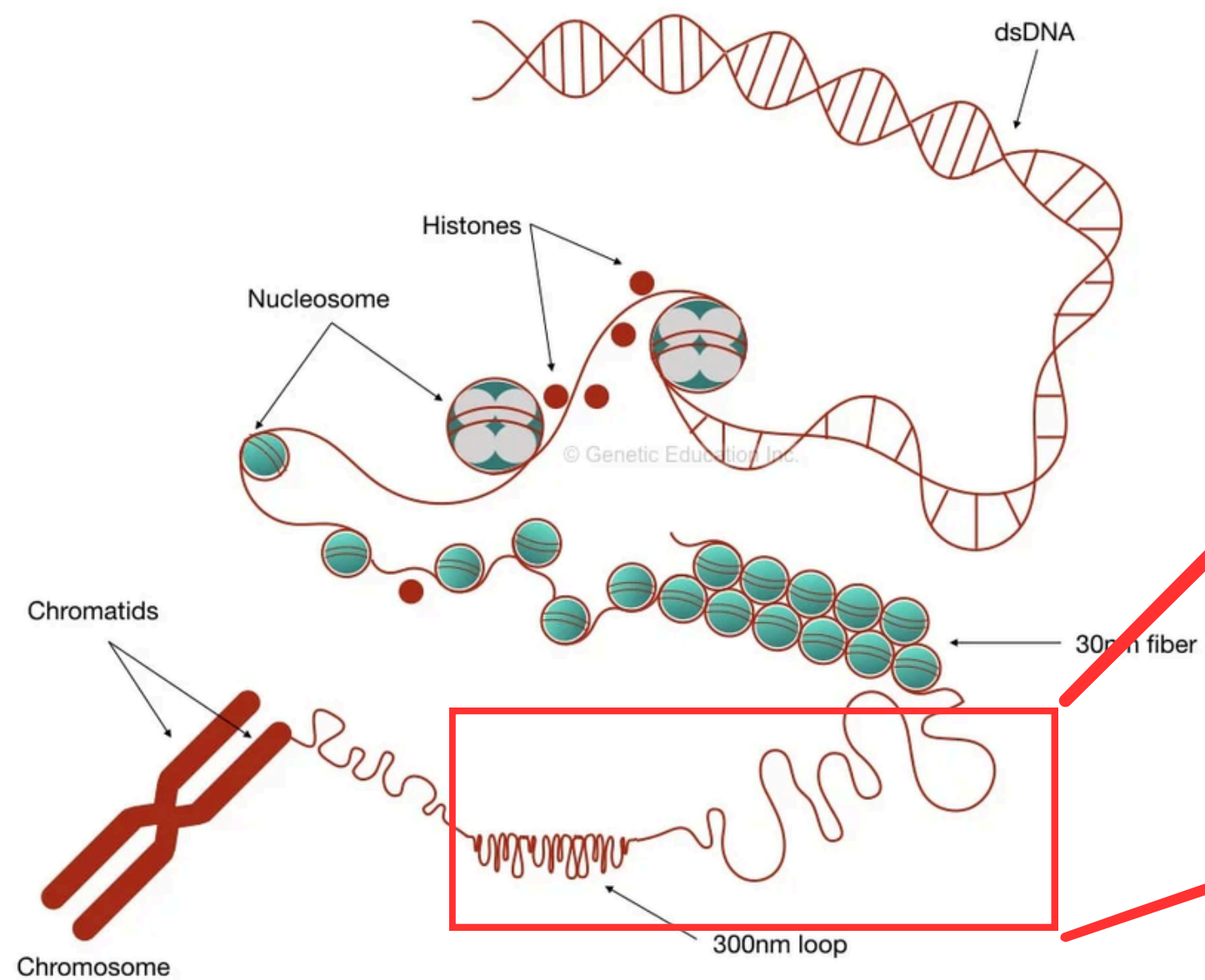


Hypothesis II





Hypothesis II



$$i\hbar \frac{\partial}{\partial t} |\psi(t)\rangle = \hat{H} |\psi(t)\rangle$$

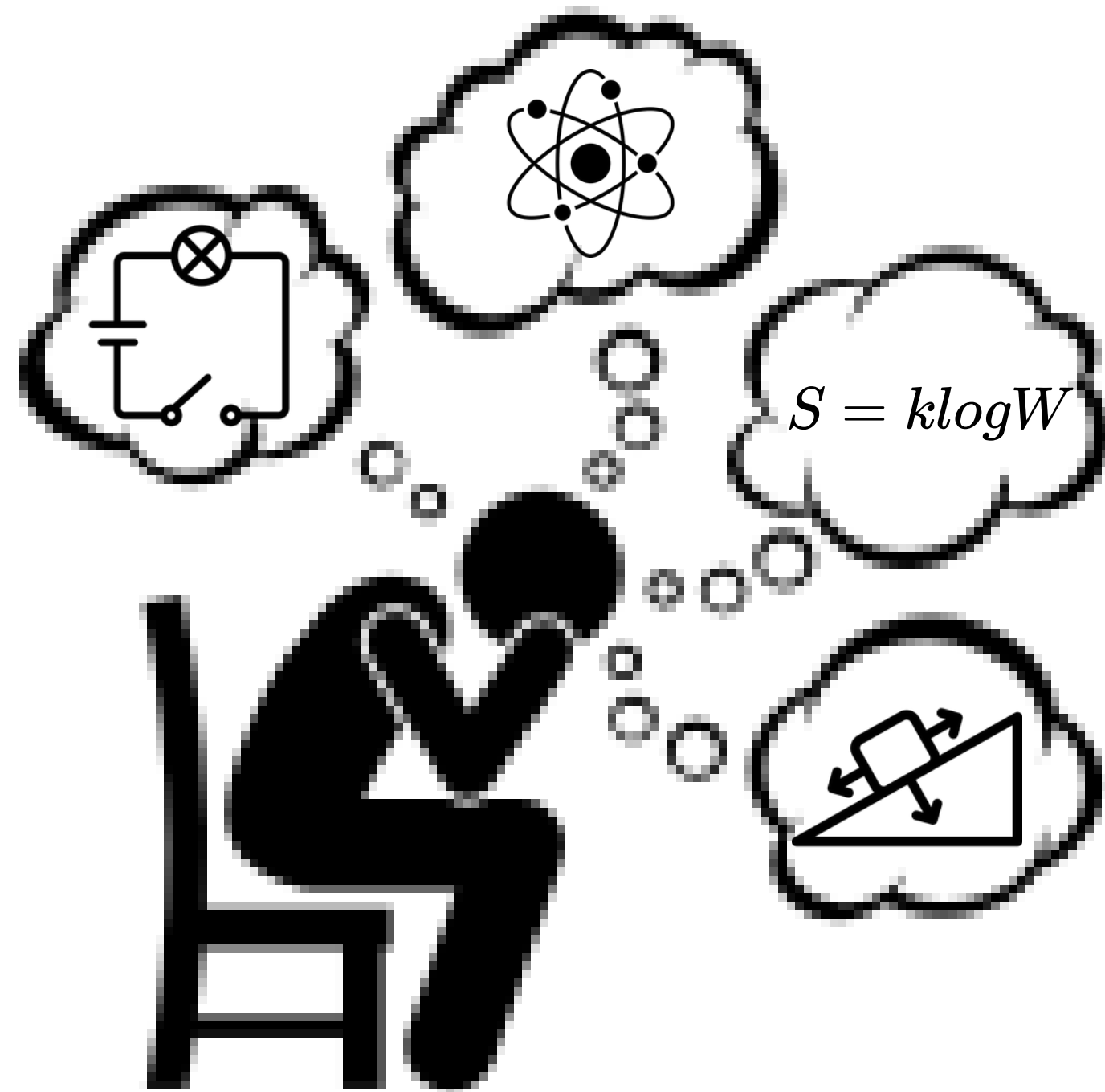


Quantum mechanics?



DNA sequencing and physics

How can we solve the problem?

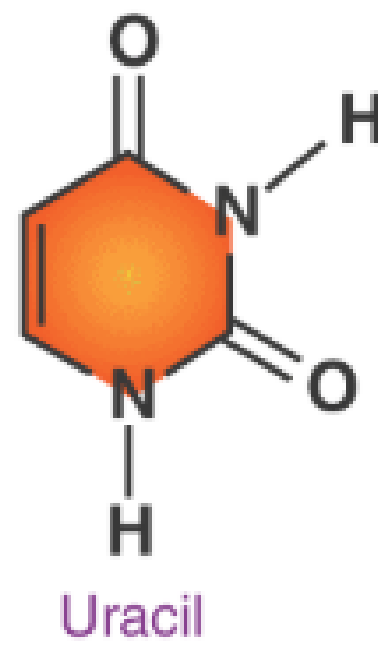
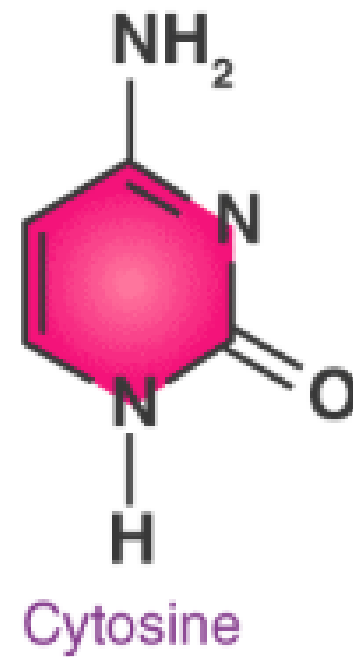
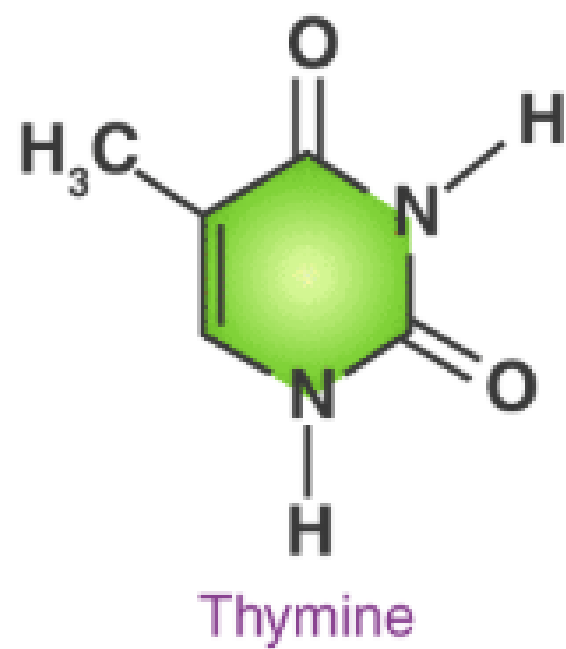
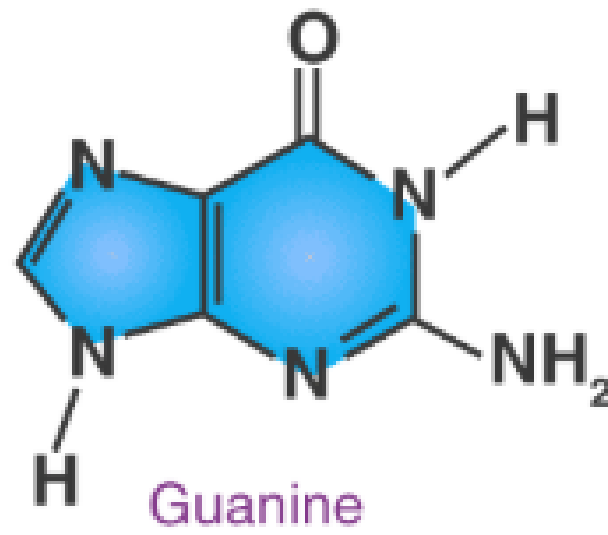
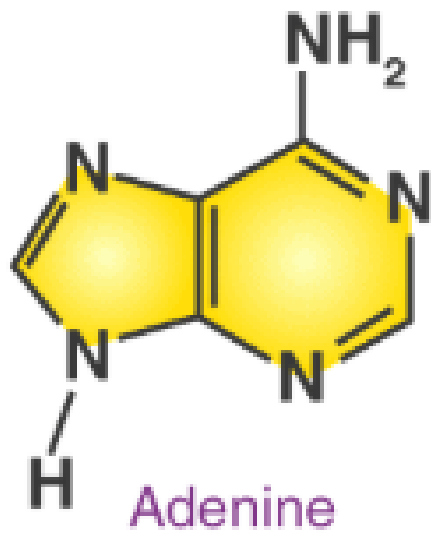




Each nucleotide has
a characteristic
structure



Nucleotides



How to identify
nucleotides based on
their **shapes**?



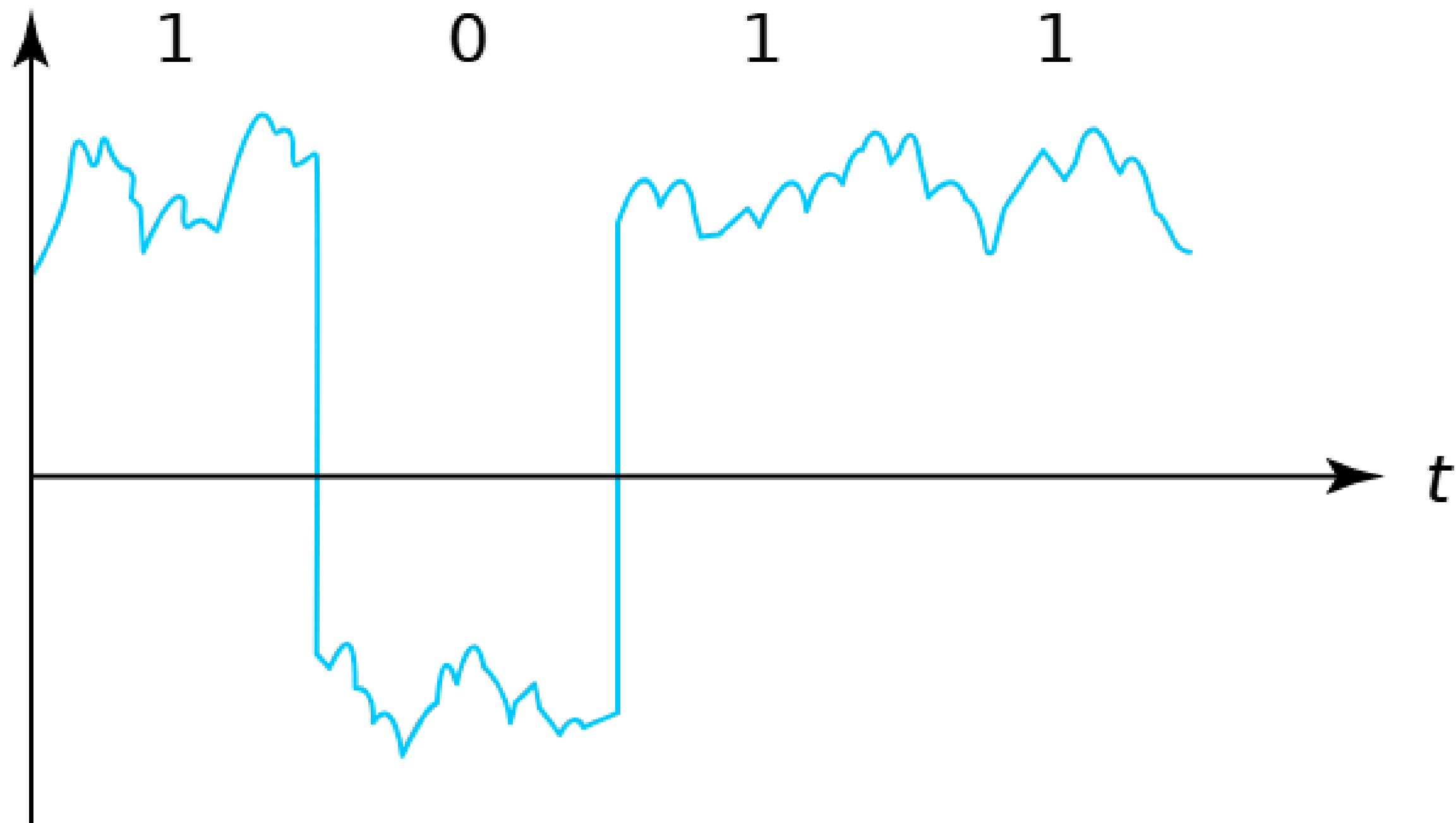
Looking for foodprints



We need the snow!



Electric signal





Looking for footprints

Too many footprints!





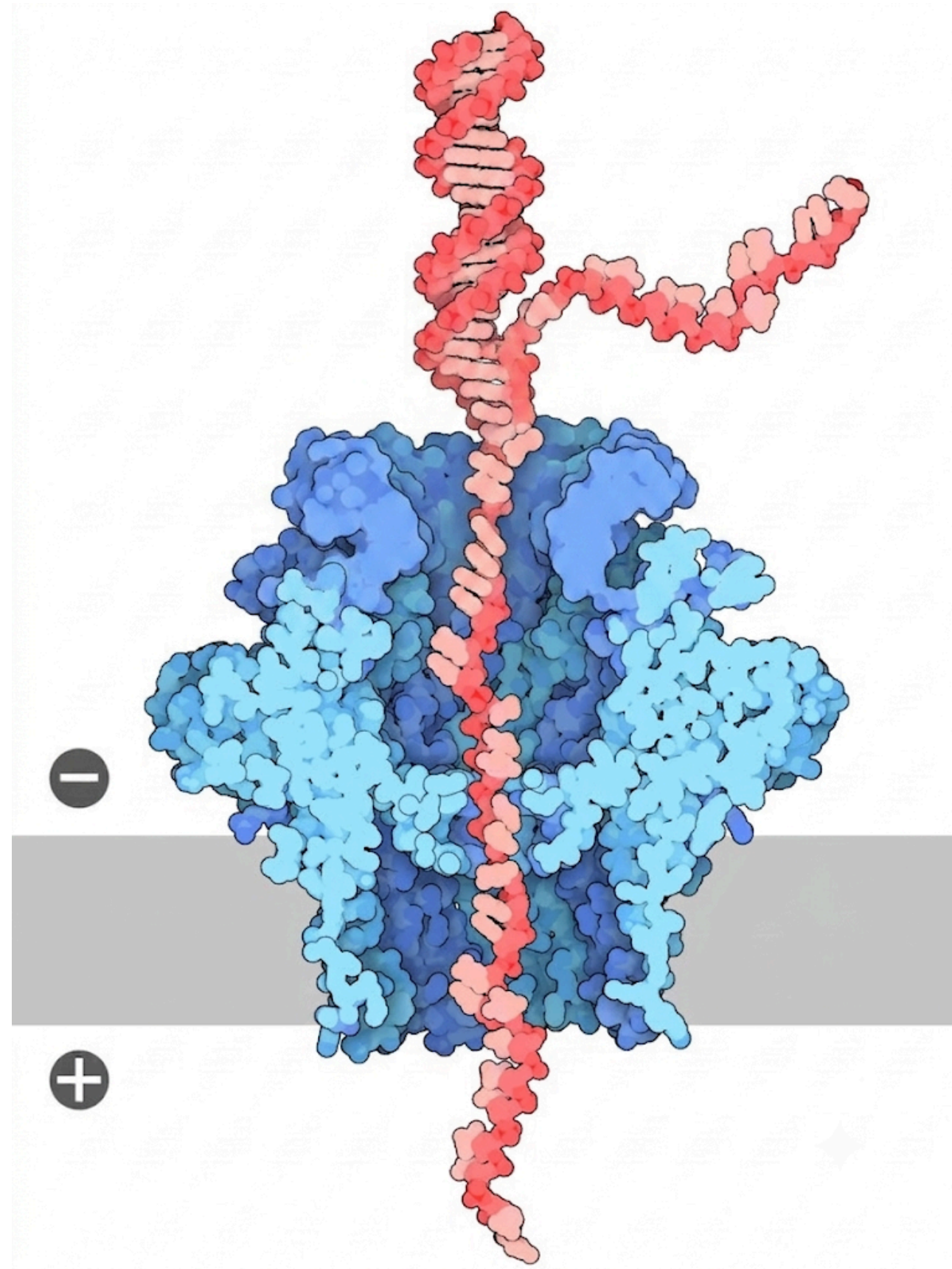
An orderly queue



We need a turnstile!



A nanopore





Slowing down the queue

But the process is very noisy.



Slowing down the queue

But the process is very noisy.

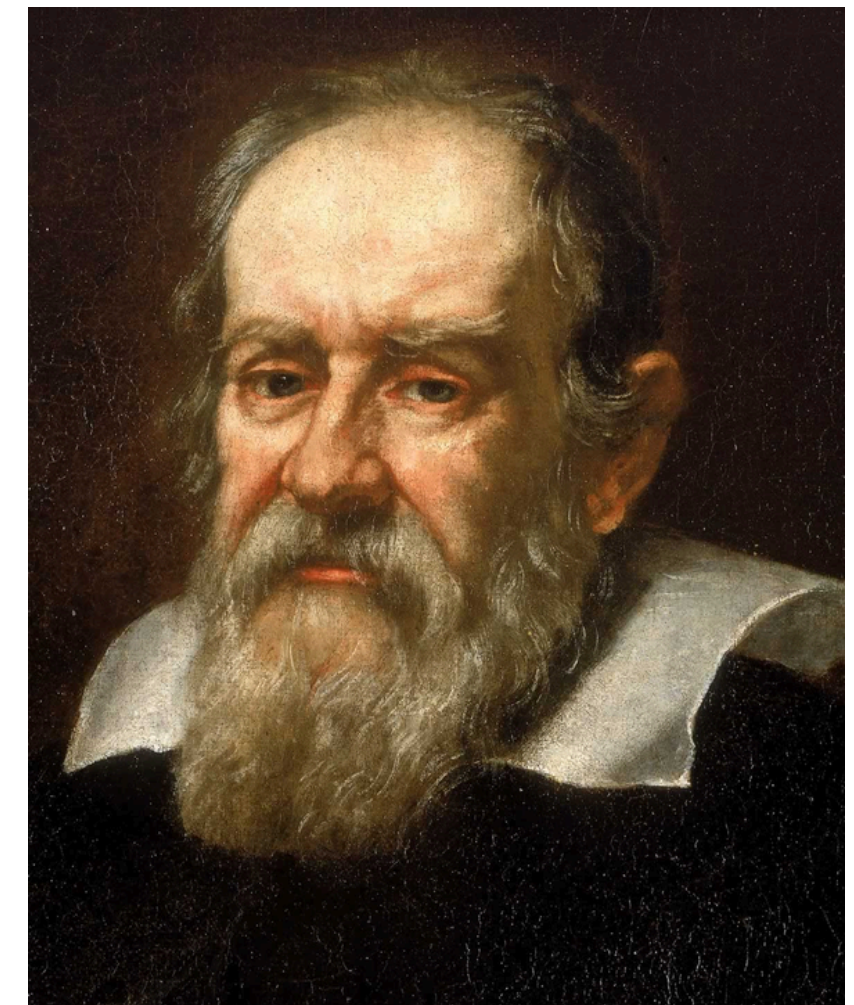
We need to slow down it (as Galileo teaches)



Slowing down the queue

But the process is very noisy.

We need to slow down it (as Galileo teaches)

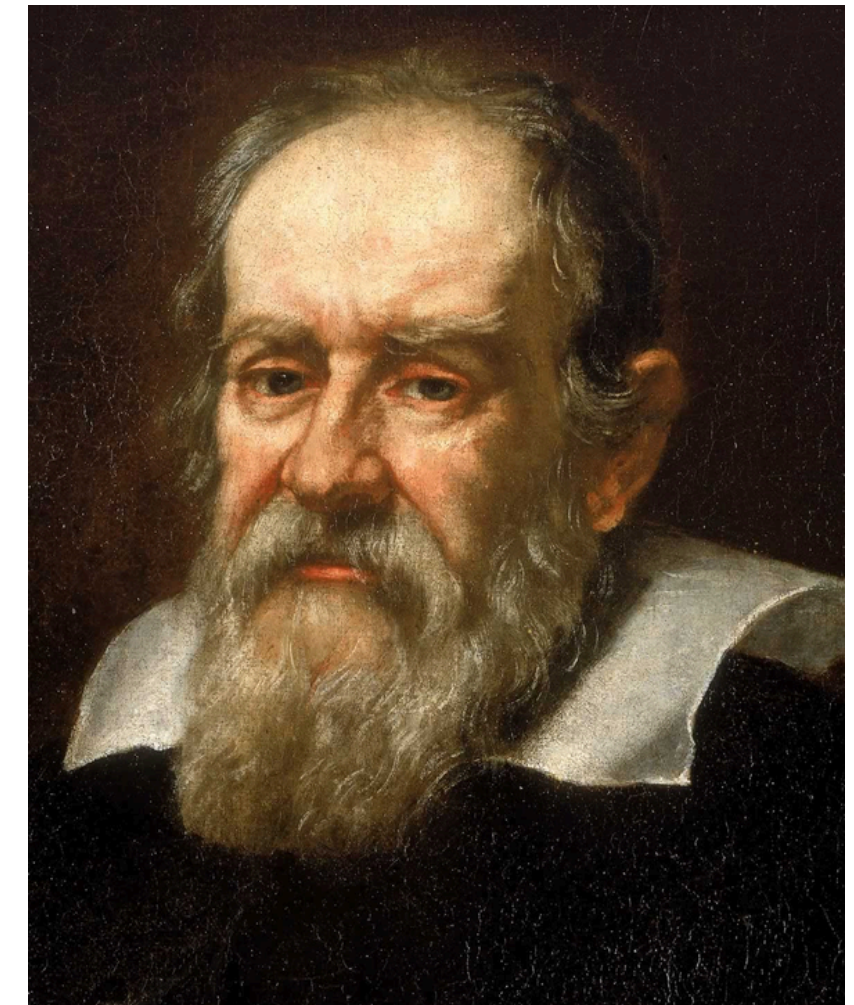
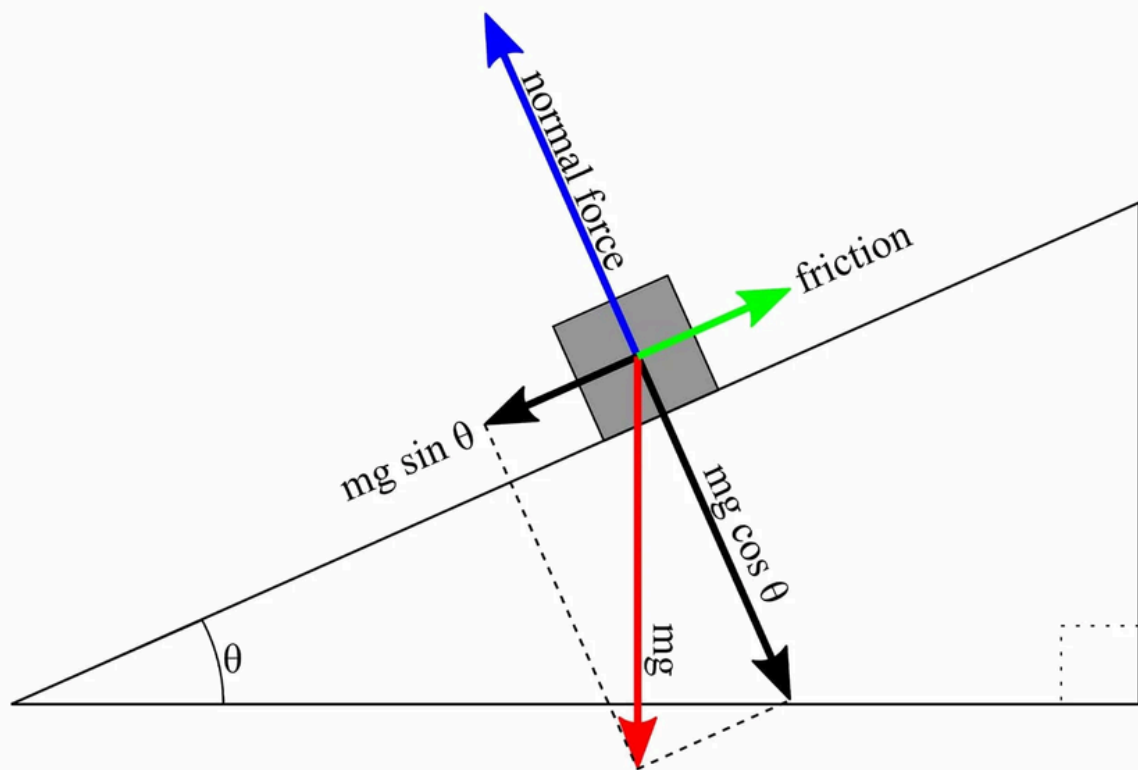




Slowing down the queue

But the process is very noisy.

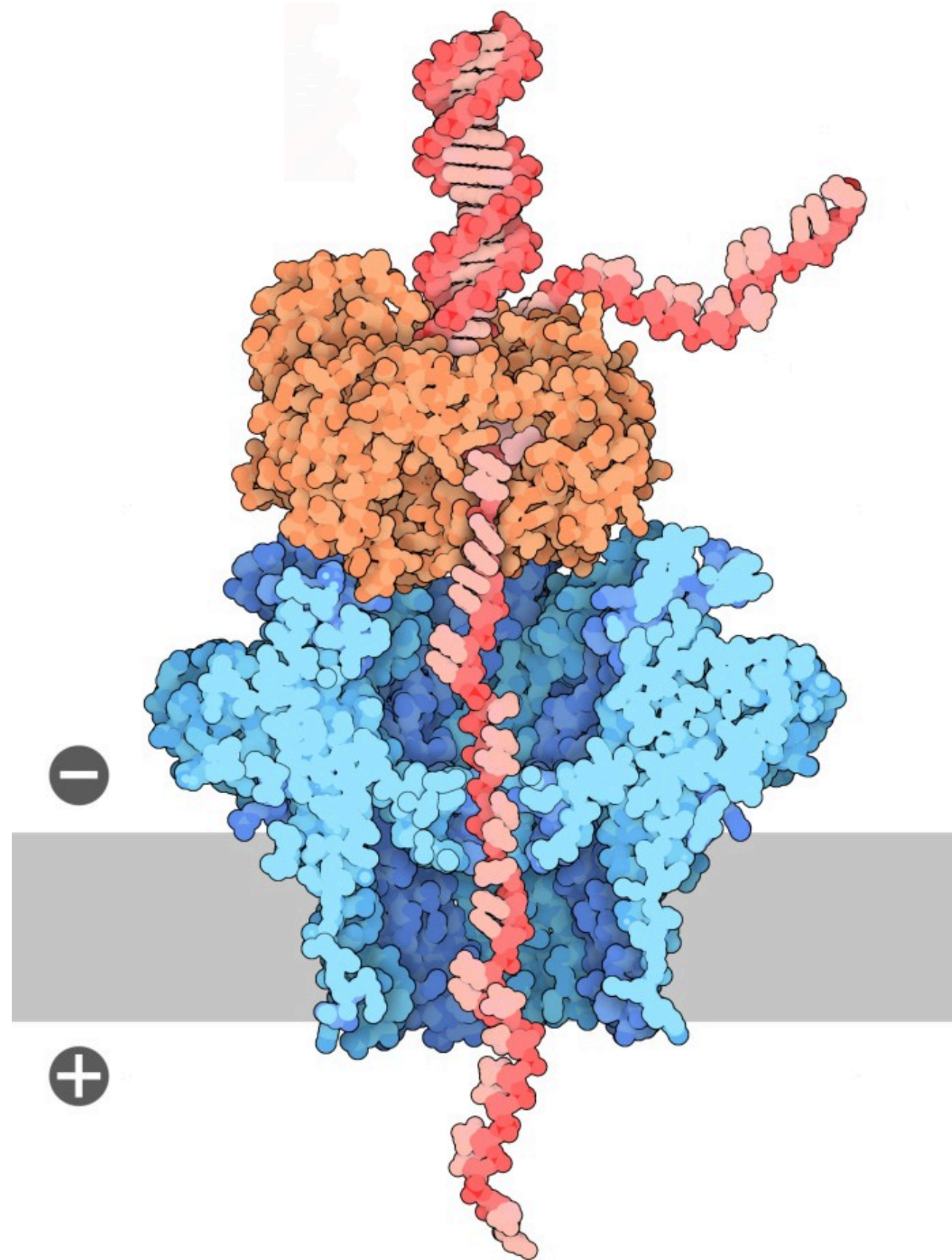
We need to slow down it (as Galileo teaches)



We need the inclined plane!



A motor protein





The first sketch (1989)

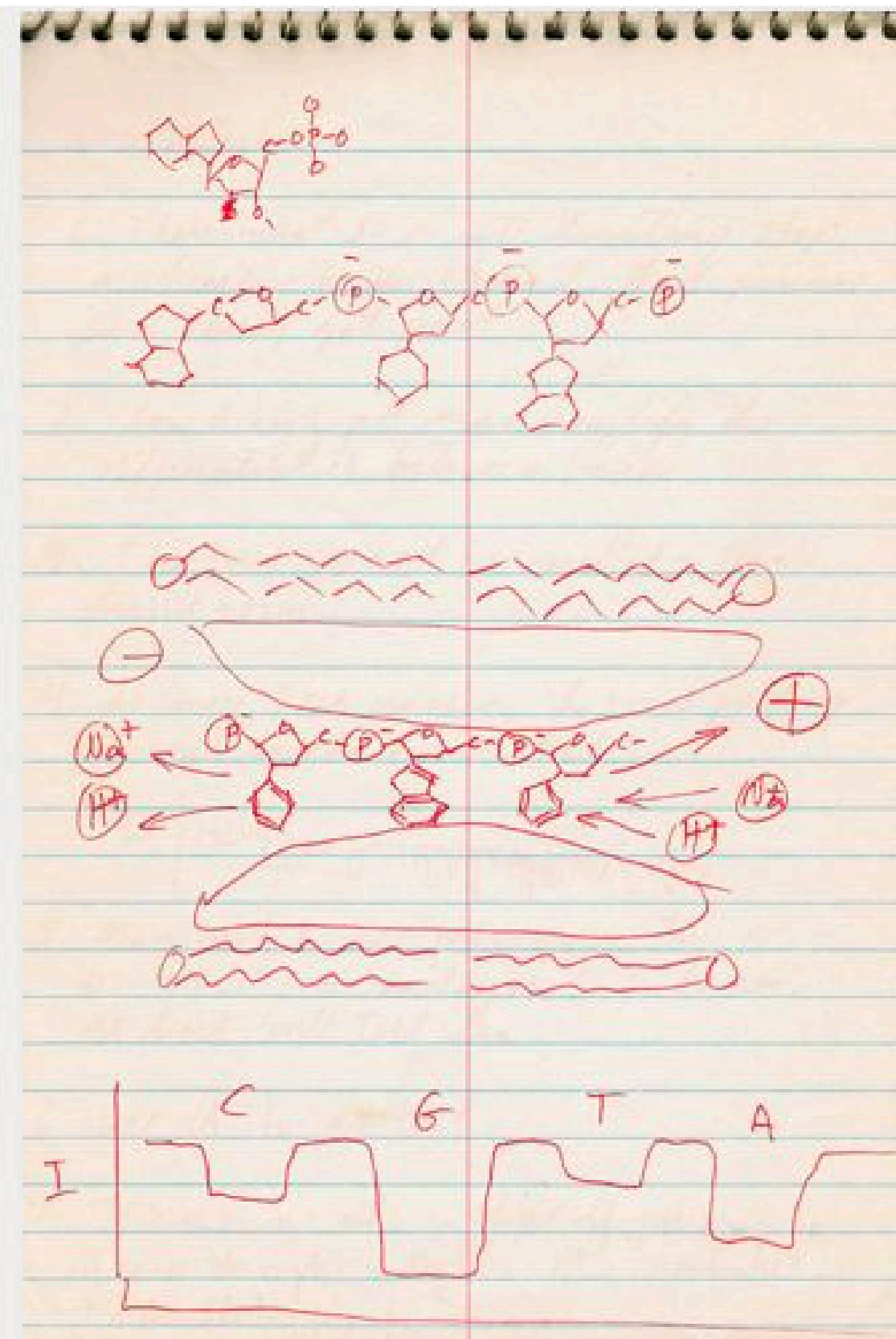
Sunday June 25, 1989
 Driving back from Eugene → Belknap
 Lodge, had an idea on how to sequence
 DNA directly:

Main concept:

DNA will be driven through a small
 channel, either by $\Delta\psi$ or ΔpH . The channel
 will be carrying a current, driven by $\Delta\psi$.
 as each base passes through, a change
 in the current will occur. Because the
 bases are of different size, the current
 change will be proportional, thereby
 providing an indication of which base
 it is.

Details:

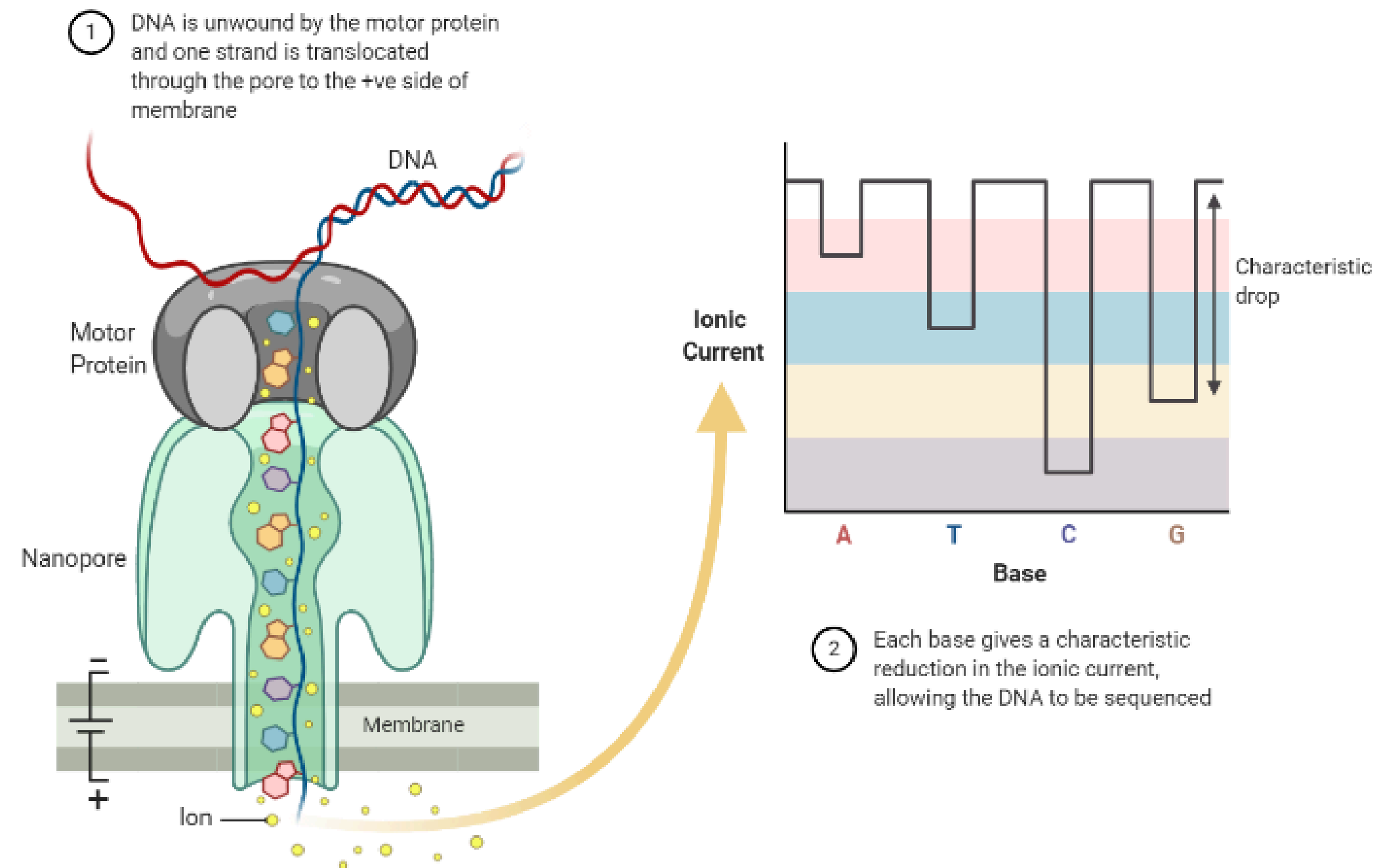
The thickness of the membrane must
 be very thin, perhaps a polymerized bilayer.
 The channel must be of the dimensions
 of DNA in cross section, approx. 1-2 nm.
 Porin? Complement? Alamethicin?
 The ion flux might be protonic.





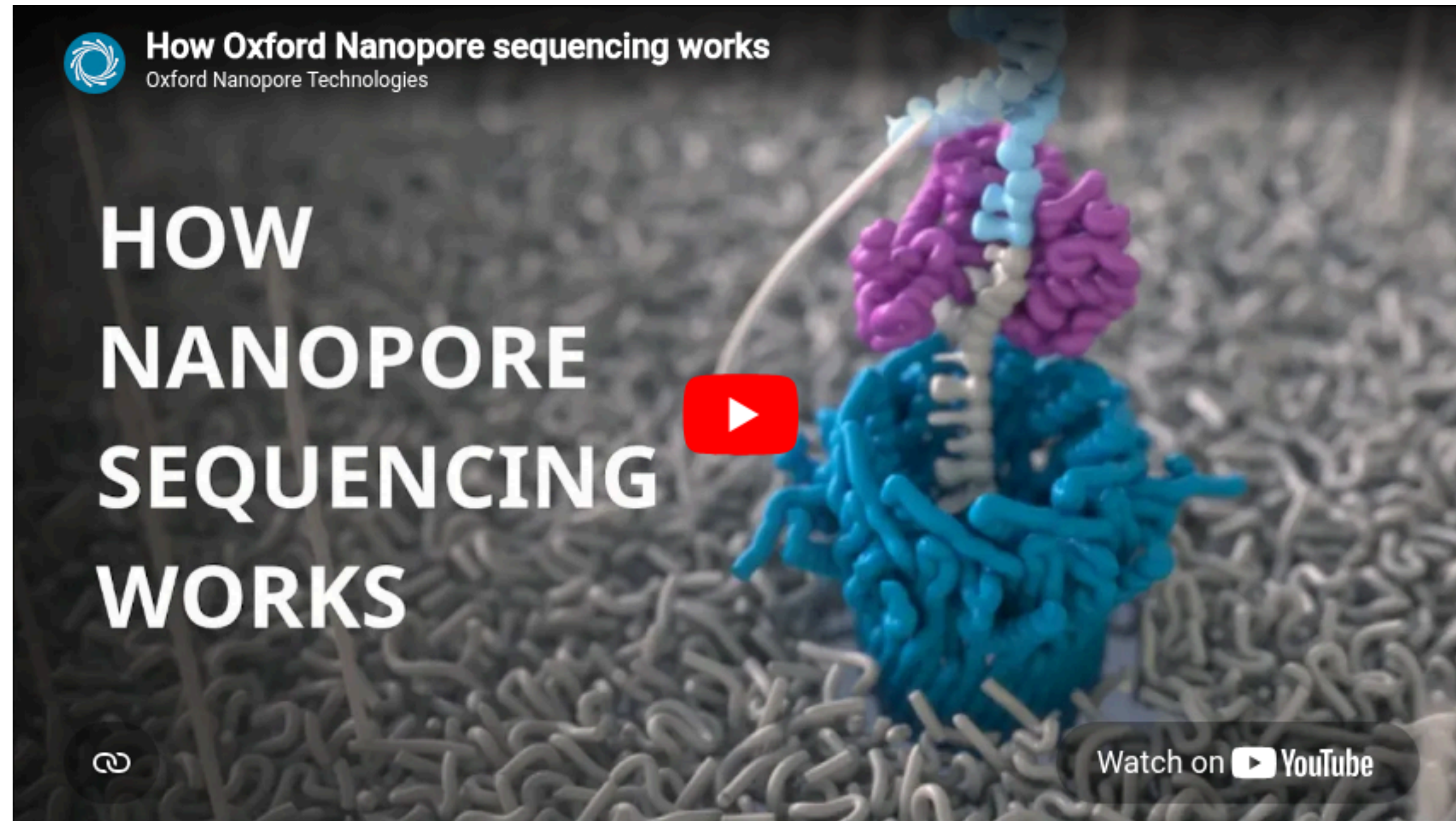
Nanopore sequencing

Nanopore Sequencing





Nanopore sequencing



https://www.youtube.com/watch?v=VxGliKyYuFQ&list=PLxpxXZj-IgXy1HCVBIDY8JzzzSSXo4c_j



Nanopore sequencing

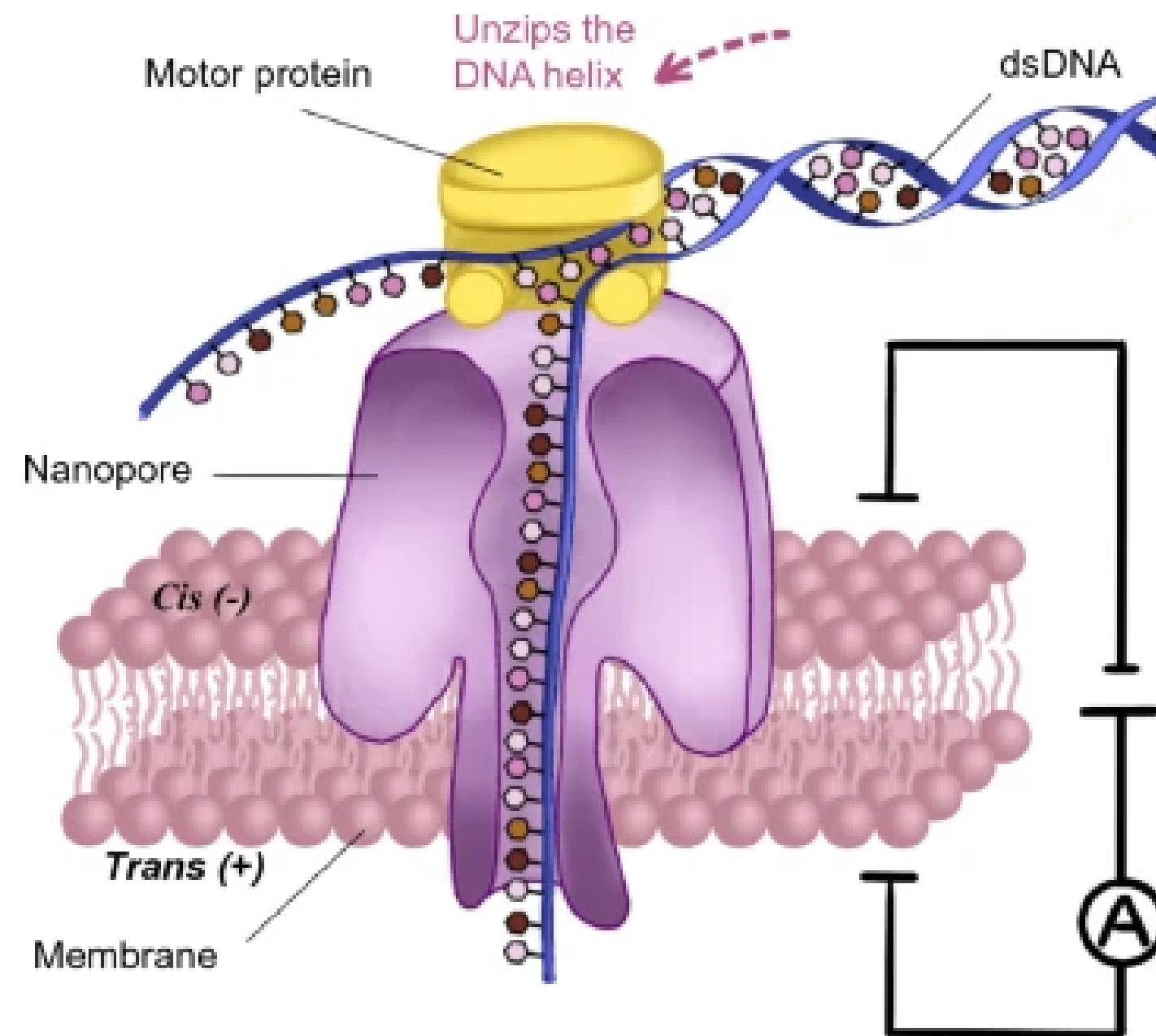


Current detection

DNA sequencing



Setup



$$R_{pore} \approx 2nm$$

$$L_{pore} \approx 10nm$$

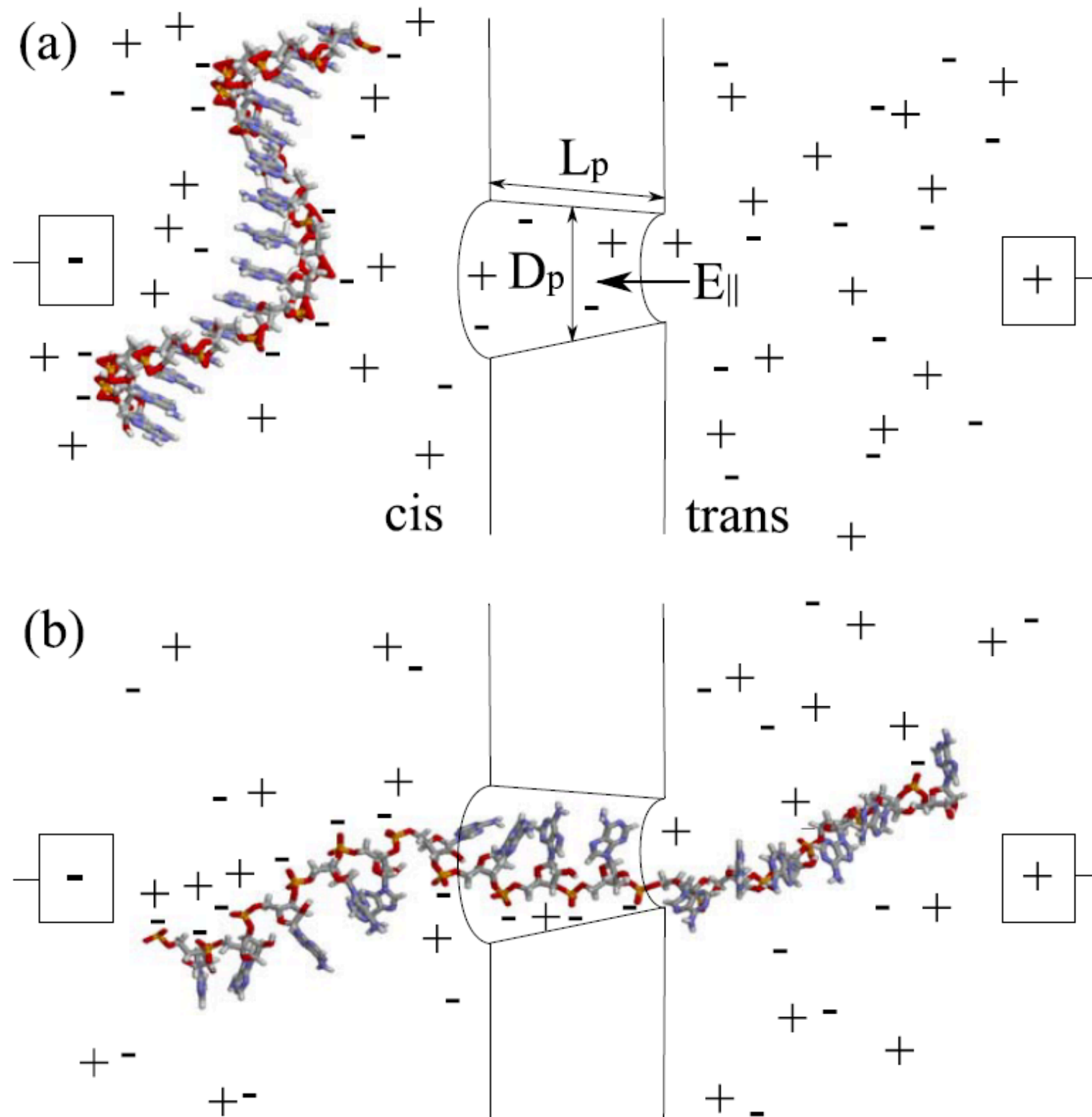
$$V \approx 100mV$$

$$z_{eff} \approx -0.5e$$

$$E_z = \frac{V}{L_{pore}} \approx 10^7 Vm^{-1}$$



Let's go through physics



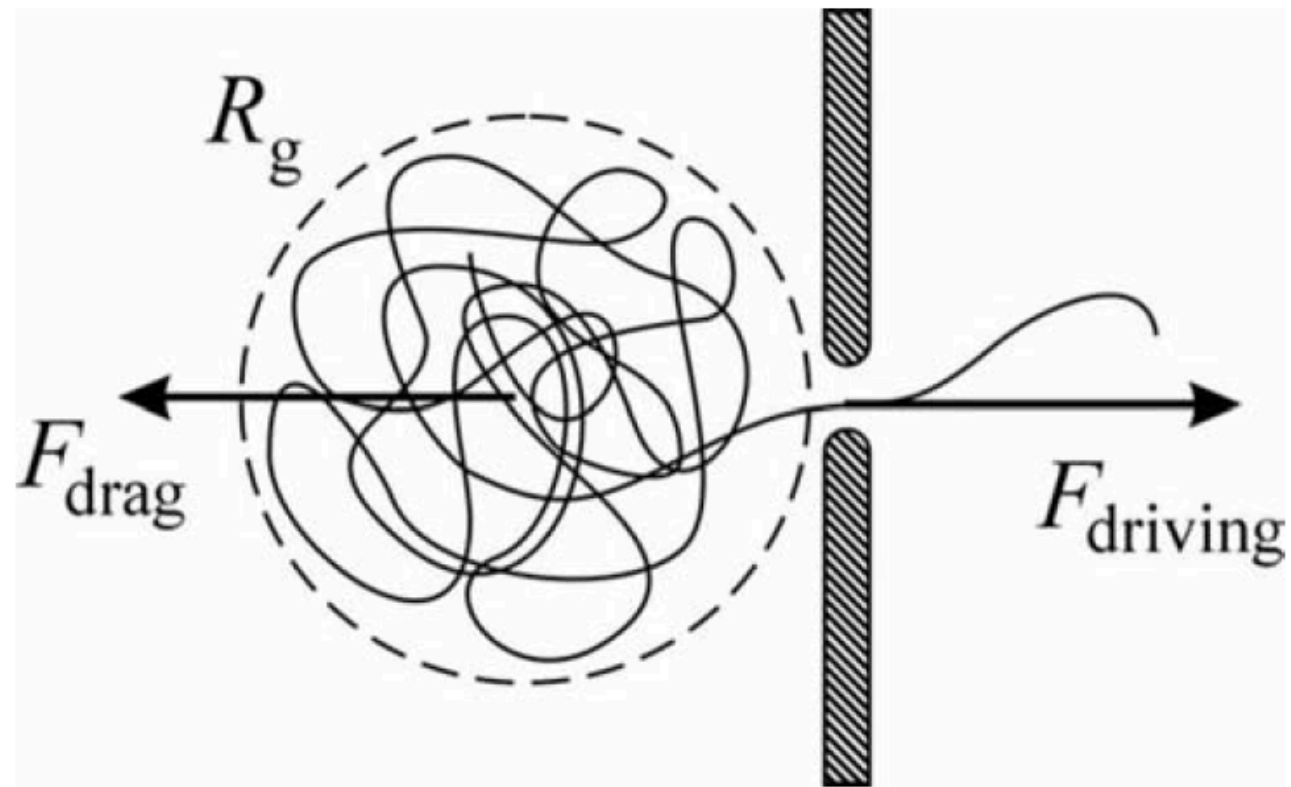
An isolating membrane separates two chambers (*cis* and *trans*) with electrolytic solution and **applied voltage**

DNA is negatively charged in solution (phosphate groups)



DNA motion

The DNA motion is governed by several effects:

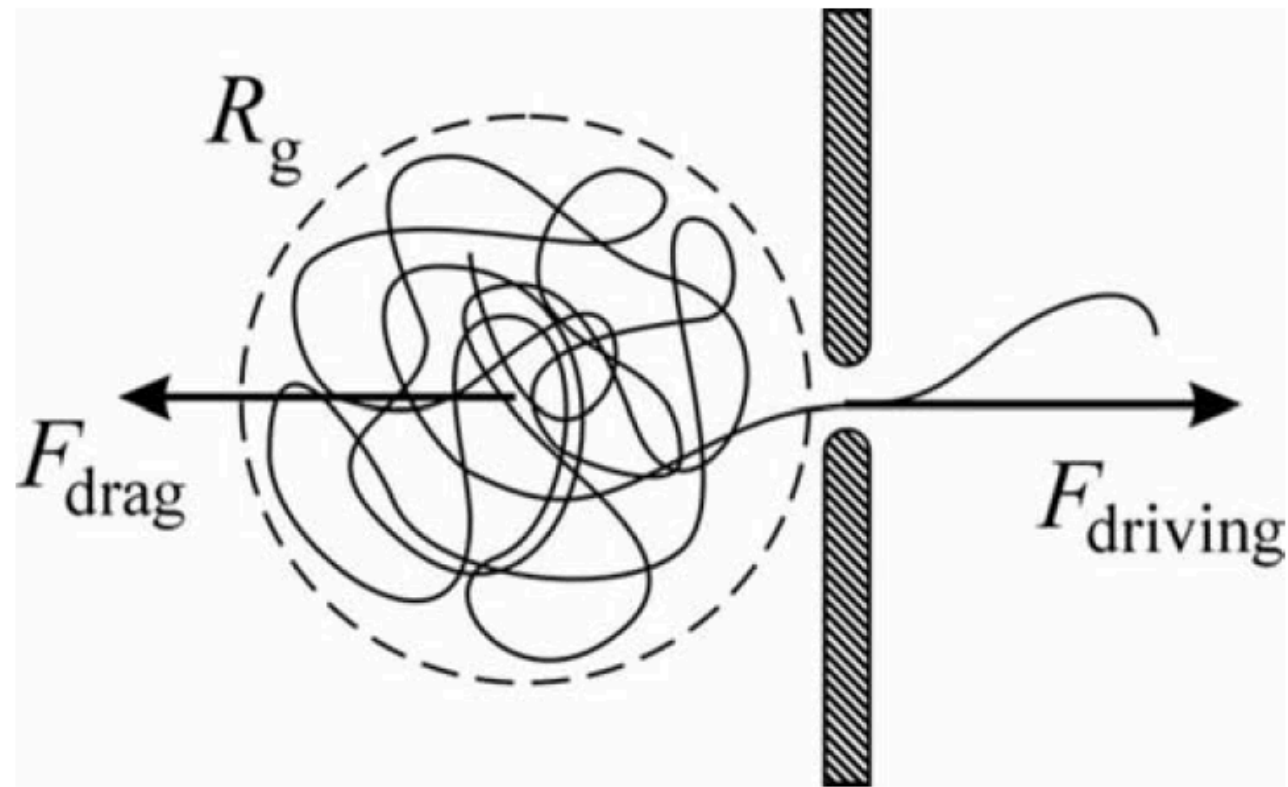




DNA motion

The DNA motion is governed by several effects:

- **Electrostatic force**



$$F_{\text{driving}} = z_{\text{eff}} E_z$$



DNA motion

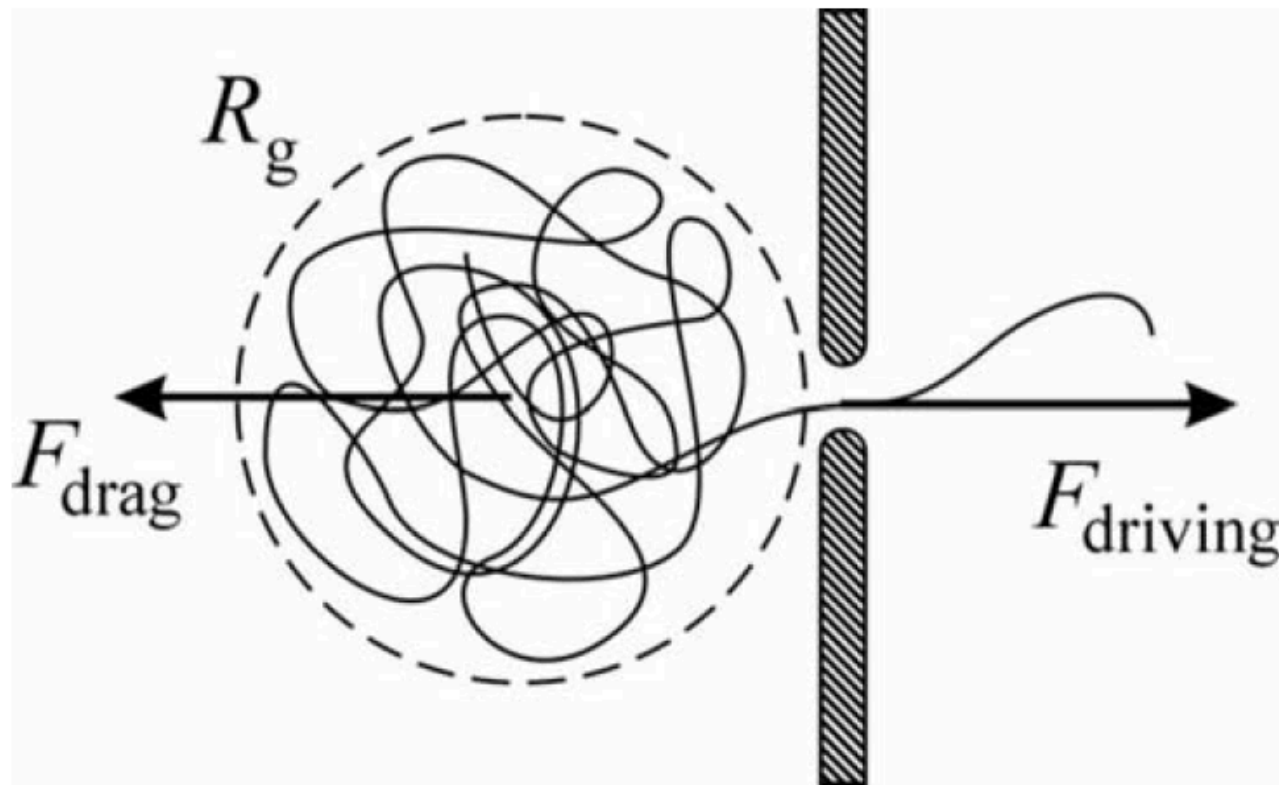
The DNA motion is governed by several effects:

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$$F_{driving} = z_{eff} E_z$$

- **Hydrodynamic drag of the external polymer**

$$F_{drag} = \eta v$$





DNA motion

The DNA motion is governed by several effects:

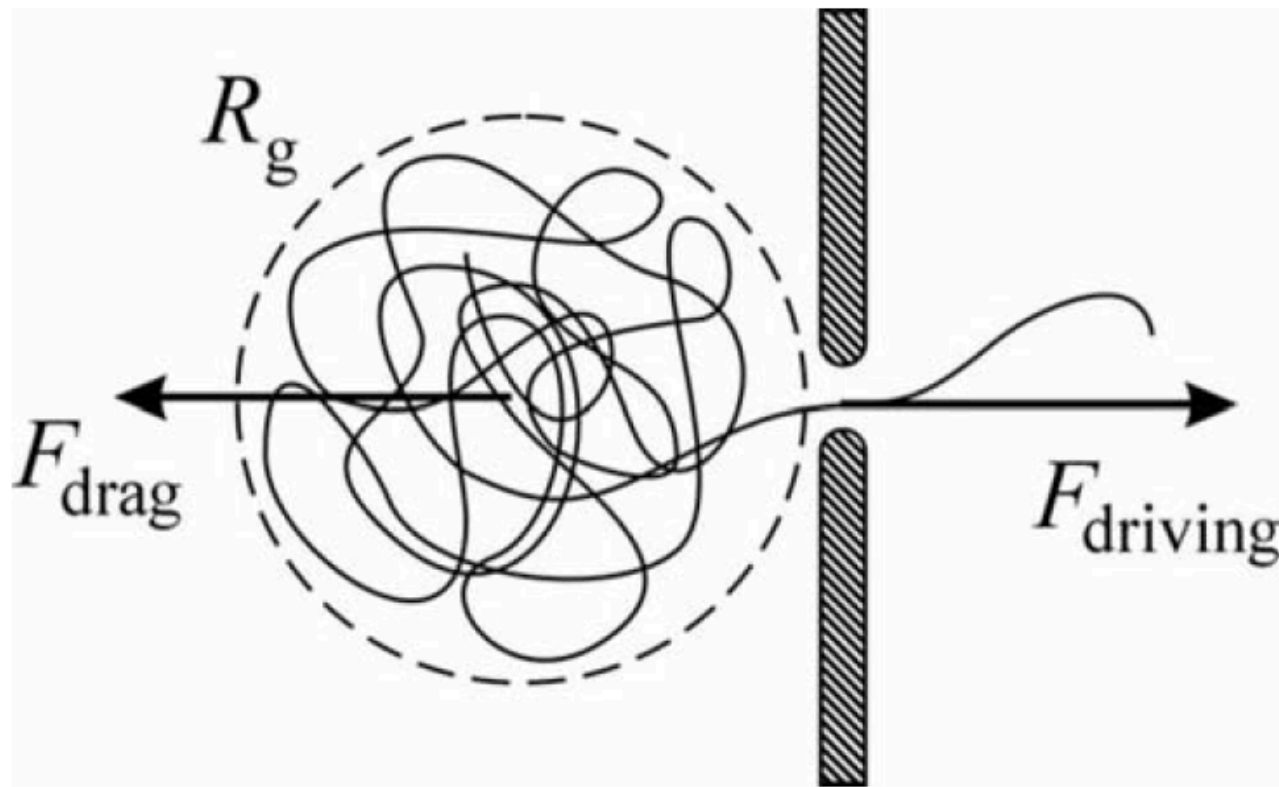
- **Electrostatic force**

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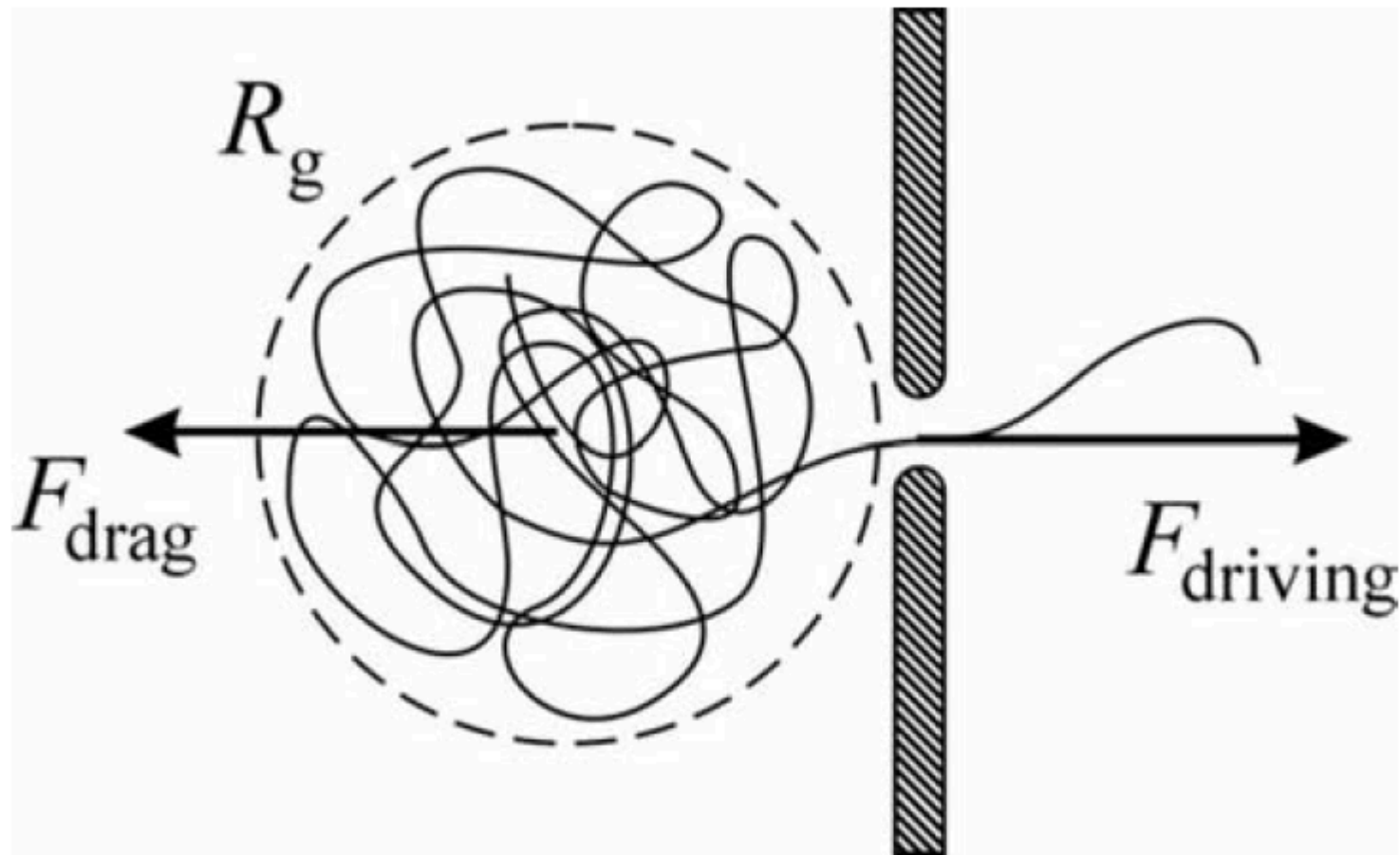
$$F_{drag} = \eta v$$

- **Entropic barrier** (DNA must uncoil to enter the nanopore)





Stationary state

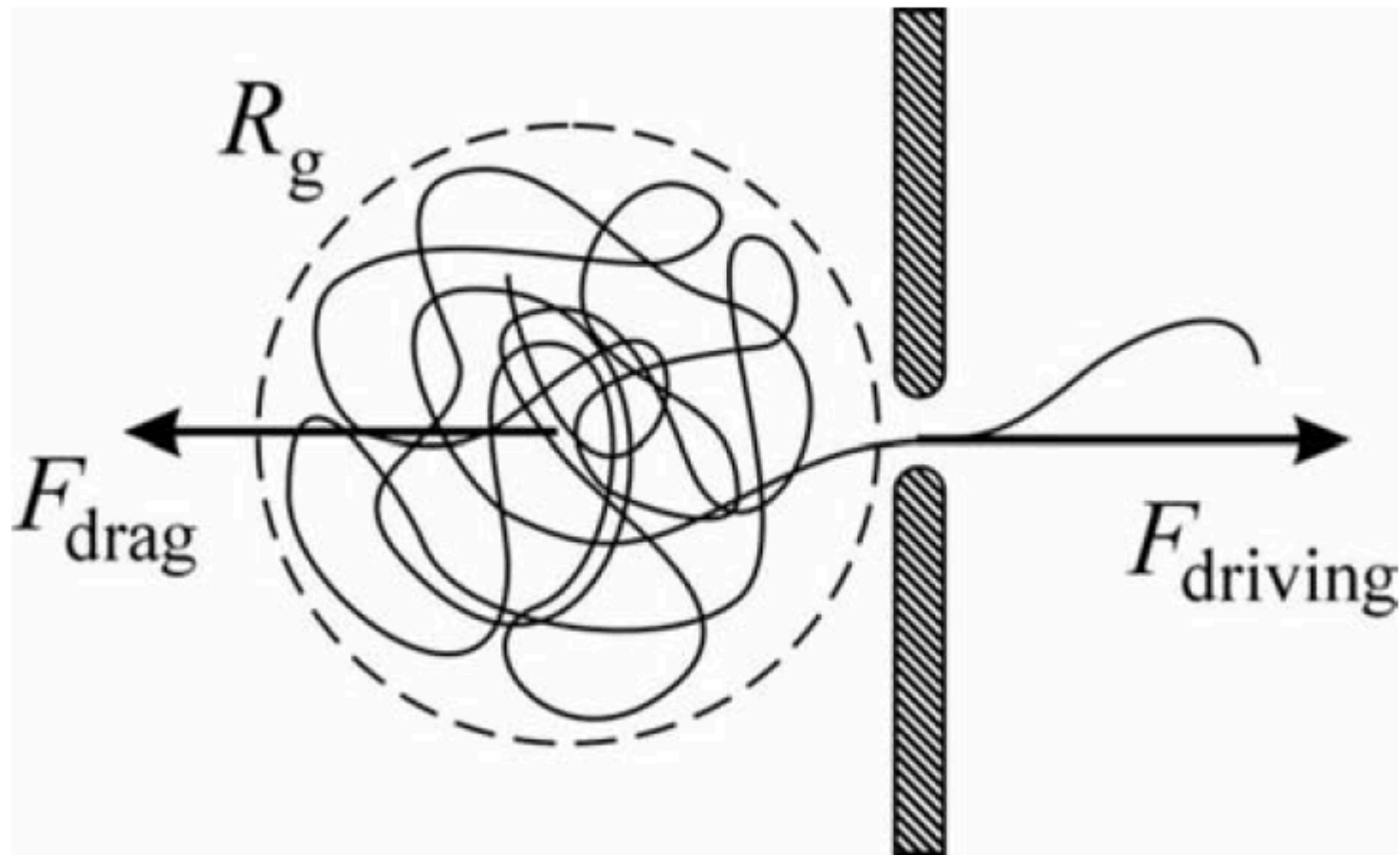


$$F_{\text{drag}} = F_{\text{driving}}$$

$$v = \frac{z_{\text{eff}}}{\eta} E_z$$



Stationary state



$$F_{drag} = F_{driving}$$

$$v = \frac{z_{eff}}{\eta} E_z$$

$$v \approx \frac{2.3 \times 10^{-11}}{9 \times 10^{-11}} \approx 0.25 ms^{-1}$$

The DNA will transverse the nanopore in 40 ns!



Ionic current

How the volume exclusion affect the blockade current?



Ionic current

How the **volume exclusion** affect the blockade current?

$$J_z = e\mu n E_z - eD \frac{dn}{dz}$$

Nernst-Planck
equation



Ionic current

In absence of any dominant diffusive terms, the open pore current is

$$I_0 = e\mu n E_z$$



Ionic current

In absence of any dominant diffusive terms, the open pore current is

$$I_0 = e\mu n E_z$$

$$I_0 \approx 13pA$$



Blockade current

The effect of volume exclusion on the ionic current can be described as

$$\frac{I_0 - I_b}{I_0} = 1 - \frac{V_{pore} - V_{nucleotide}}{V_{pore}}$$



Blockade current

The effect of volume exclusion on the ionic current can be described as

$$\frac{I_0 - I_b}{I_0} = 1 - \frac{V_{pore} - V_{nucleotide}}{V_{pore}}$$

$$I_b \approx 9 - 11 pA$$

but **differences between nucleotides are very small (1-2%)!**

Current intrinsical fluctuations are larger



Multi-base resolution

The problem is more complex

The finite-size pore sensitive region has a length comparable with some nucleotides (4-5).



Multi-base resolution

The problem is more complex

The finite-size pore sensitive region has a length comparable with some nucleotides (4-5).

Therefore, the blockade current is **a function of 4 nucleotides** (experimentally)

$$I_b = f(b_i, b_{i+1}, b_{i+2}, b_{i+3})$$



The problem of noise

Several **sources of noise** highly affect the signal detection:

- Johnson-Nyquist $S_v = 4k_bTR$
- Shot noise $S_I = 2qI$
- **Slow fluctuations** (pore, membranes, DNA strand) $S_f = \frac{1}{f}$



Single-base resolution

The idea is to map the current signal of a k-mer

Measure 1: $b_1b_2b_3b_4b_5$ (e.g. **ACCTG**)

Measure 2: $b_2b_3b_4b_5b_6$ (e.g. **CCTGT**)

Measure 3: $b_3b_4b_5b_6b_7$ (e.g. **CTGTA**)



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The single-base detection emerges from:



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The single-base detection emerges from:

- superposition of consecutive measures



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- dynamic model of translocation



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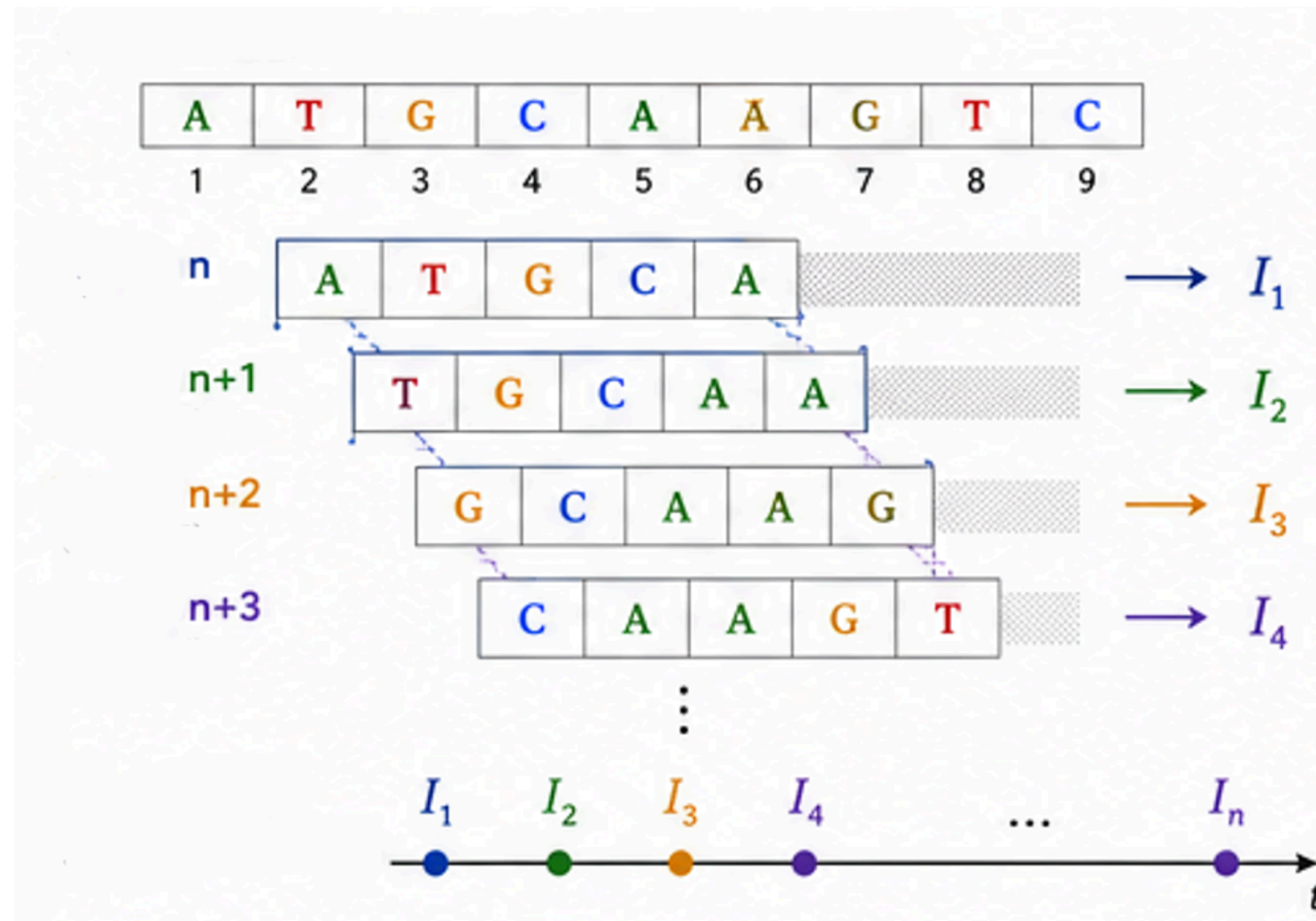
Measure 3: $b_3b_4b_5b_6b_7$ (e.g. **CTGTA**)

The single-base detection emerges from:

- superposition of consecutive measures
- dynamic model of translocation
- statistical inference

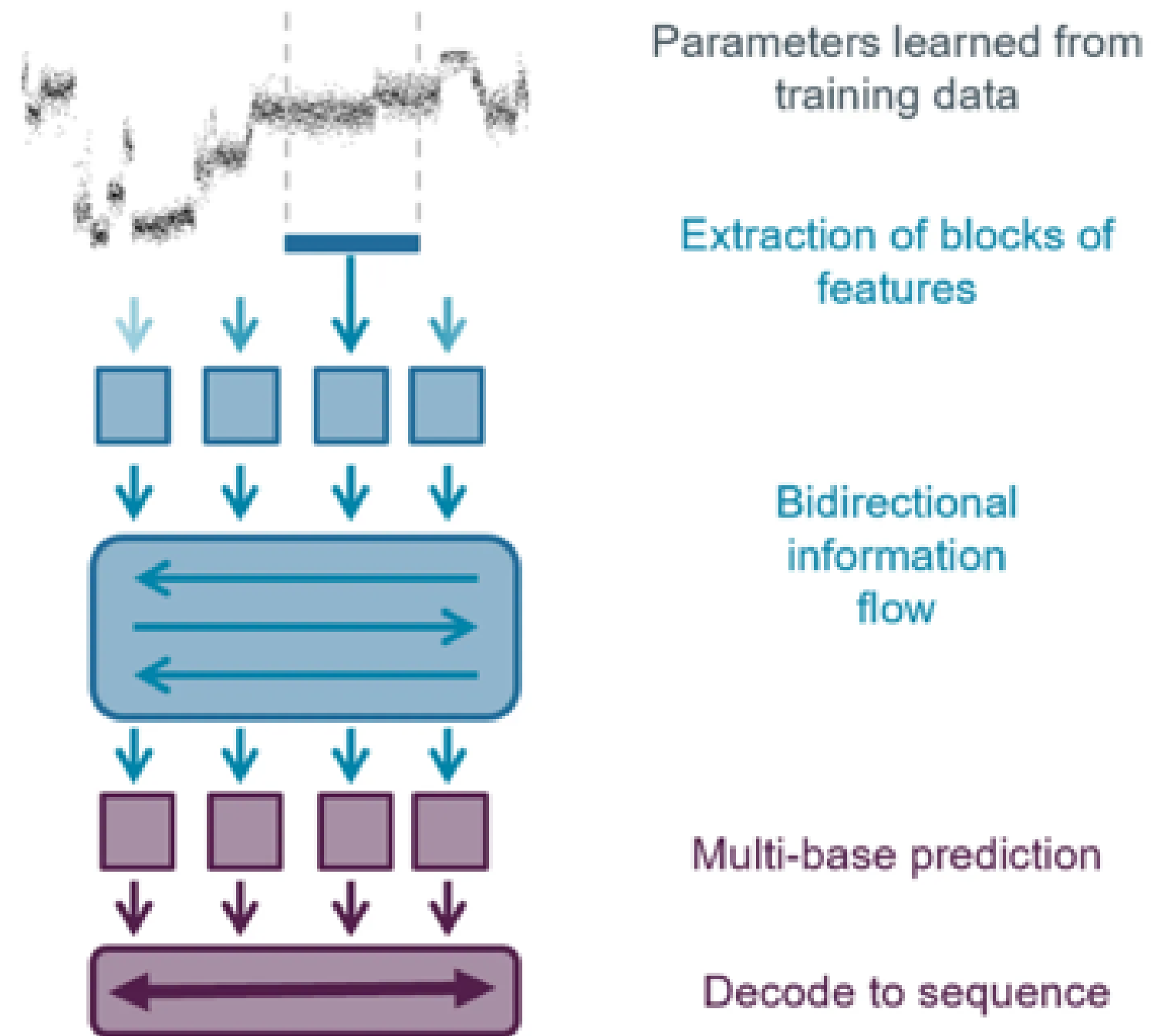


Single-base resolution





Deep Learning and nanopore sequencing



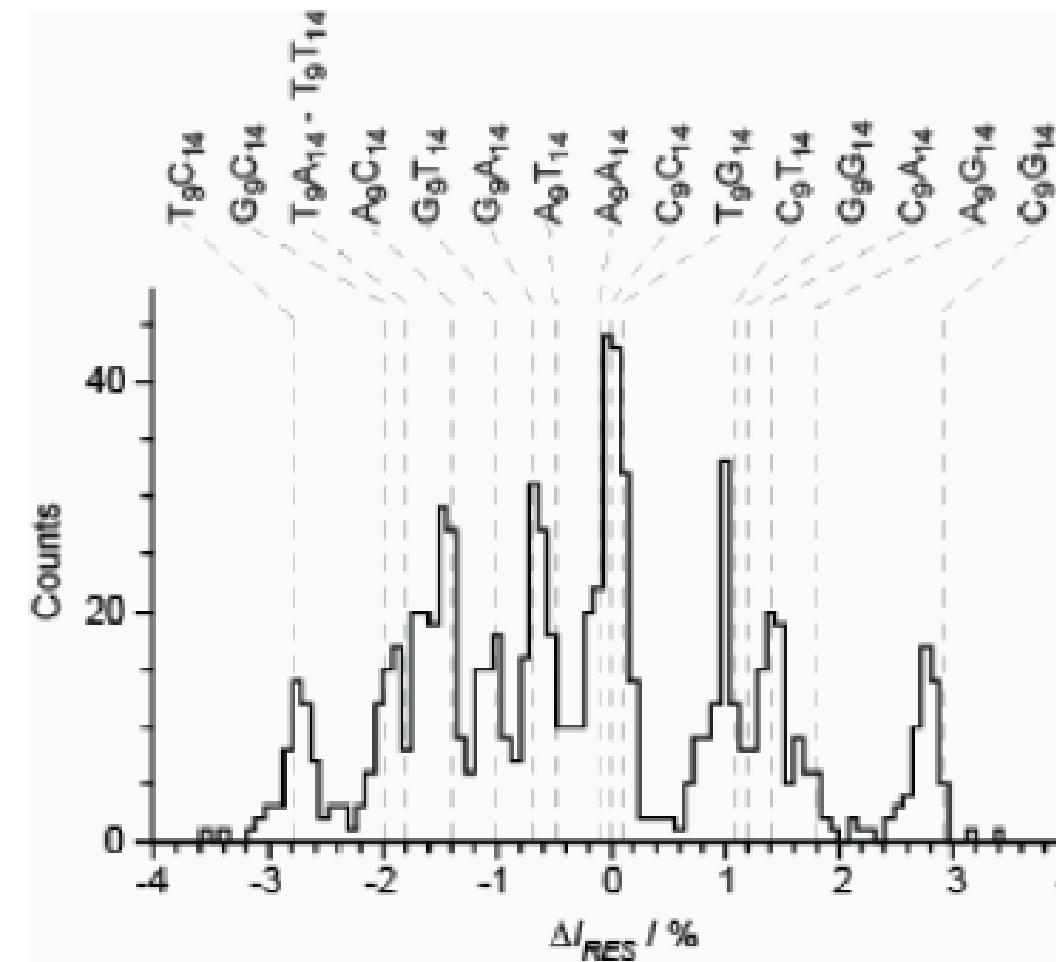
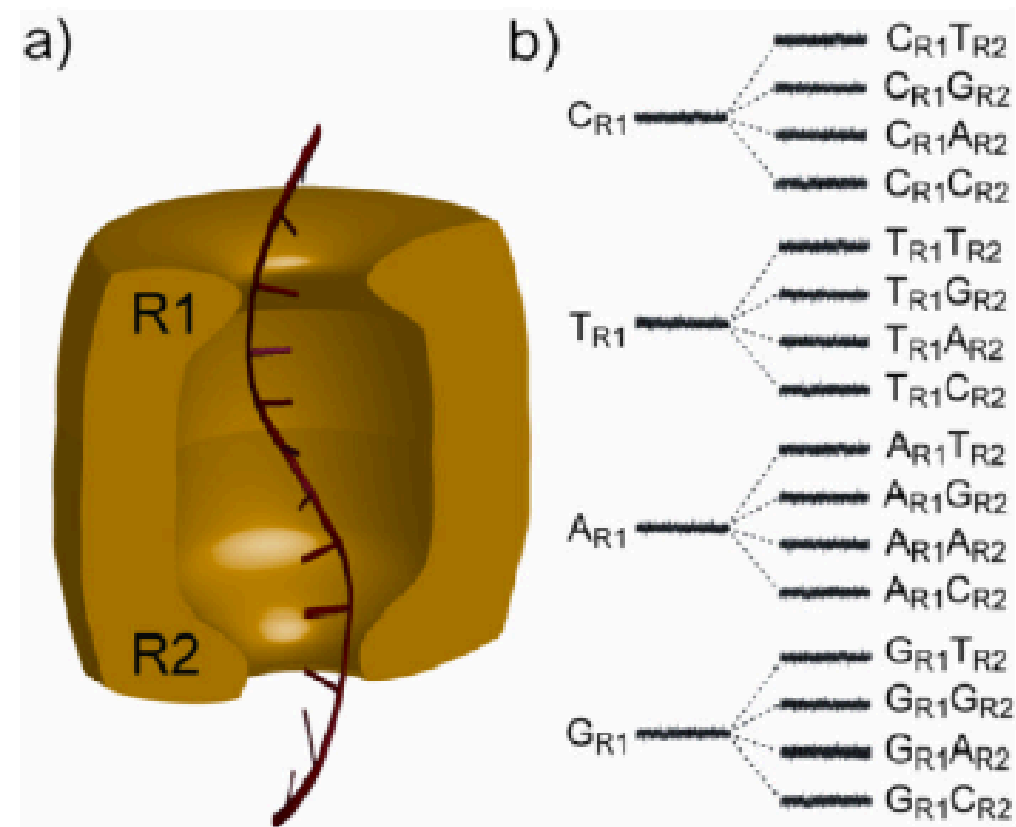
The Deep Learning model learns:

- events duration
- temporal shape
- correlations between consecutive events
- stochastic variations of the motor protein

The result is a **statistical inference from a series of correlated measures.**



Two recognition sites



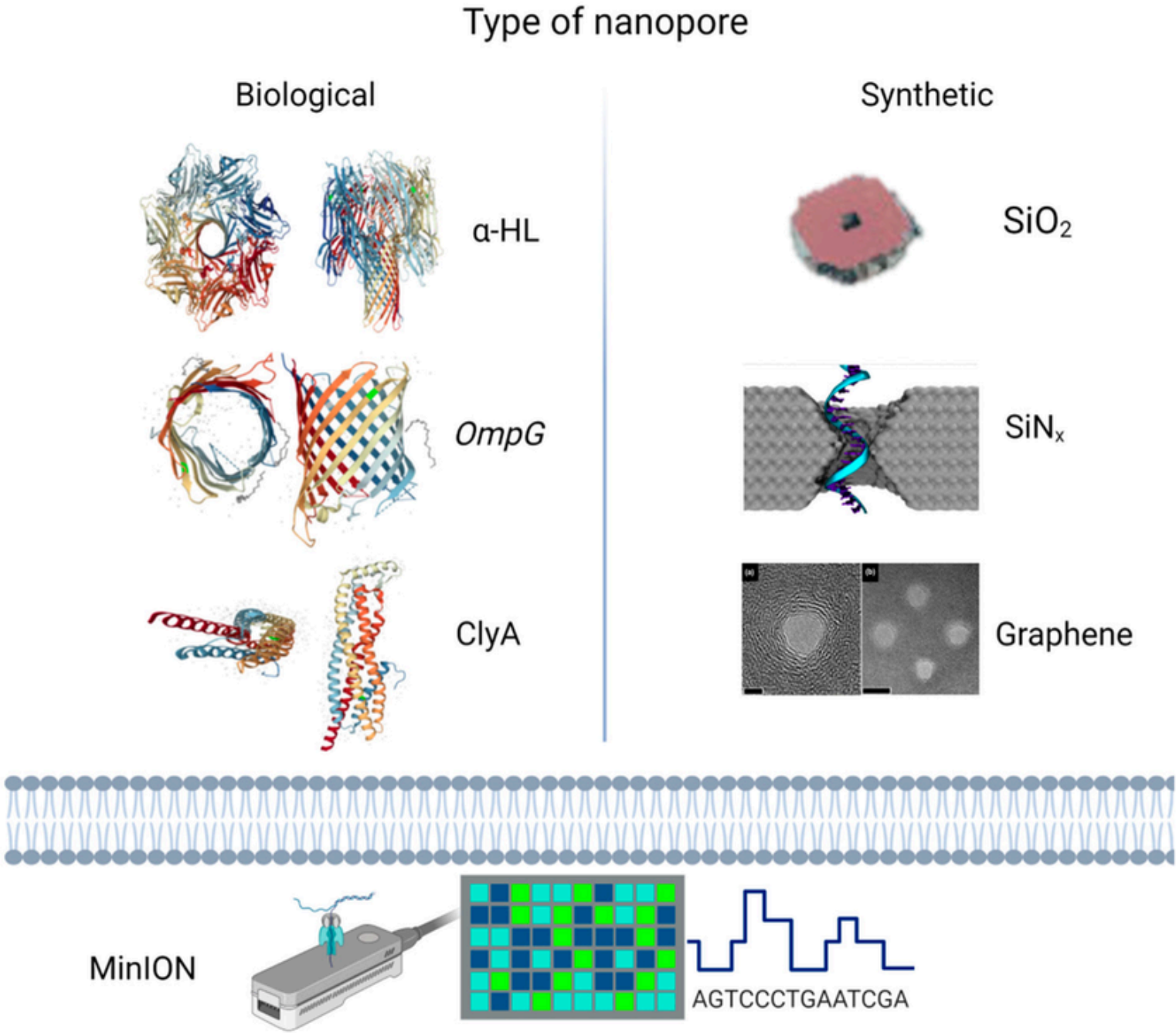
The use of **two recognition sites** in modern nanopore flow cells allows for a better resolution



Types of nanopores

Different types of nanopores can be exploited: biological and synthetic

Biological Nanopore	Structure		Critical Dimension	Types of Analytes	References
	Side View	Top View			
α -HL			1.4 nm ¹⁰⁸	small molecules, RNA, ssDNA, dsDNA, proteins	25, 28, 33, 37, 38, 41, 45, 52, 128, 129, 134-143, 148-150, 152, 153, 157
OmpG			1.3 nm ¹¹⁸	small molecules, proteins	43, 44, 125, 126
MspA			1.2 nm ¹¹⁰	ssDNA, dsDNA	31, 51, 120-122, 154-156
AeL			1.0 nm ¹¹¹	ssDNA, proteins	39, 46, 49, 127, 144, 145, 151
Phi29 Motor			3.6 nm ¹¹⁴	small molecules, ssDNA, dsDNA, proteins	48, 50, 130, 131, 146
ClyA			3.3 nm ¹¹⁶	dsDNA, proteins	40, 42, 47, 127, 132, 133, 147





Advantages of nanopore sequencing

1) Long reads



Advantages of nanopore sequencing

- 1) Long reads
- 2) Real-time sequencing



Advantages of nanopore sequencing

- 1) Long reads
- 2) Real-time sequencing
- 3) Portable sequencing



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- 4) One platform, multiple omics



Advantages of nanopore sequencing

- 1) Long reads
- 2) Real-time sequencing
- 3) Portable sequencing
- 4) One platform, multiple omics
- 5) Direct measures



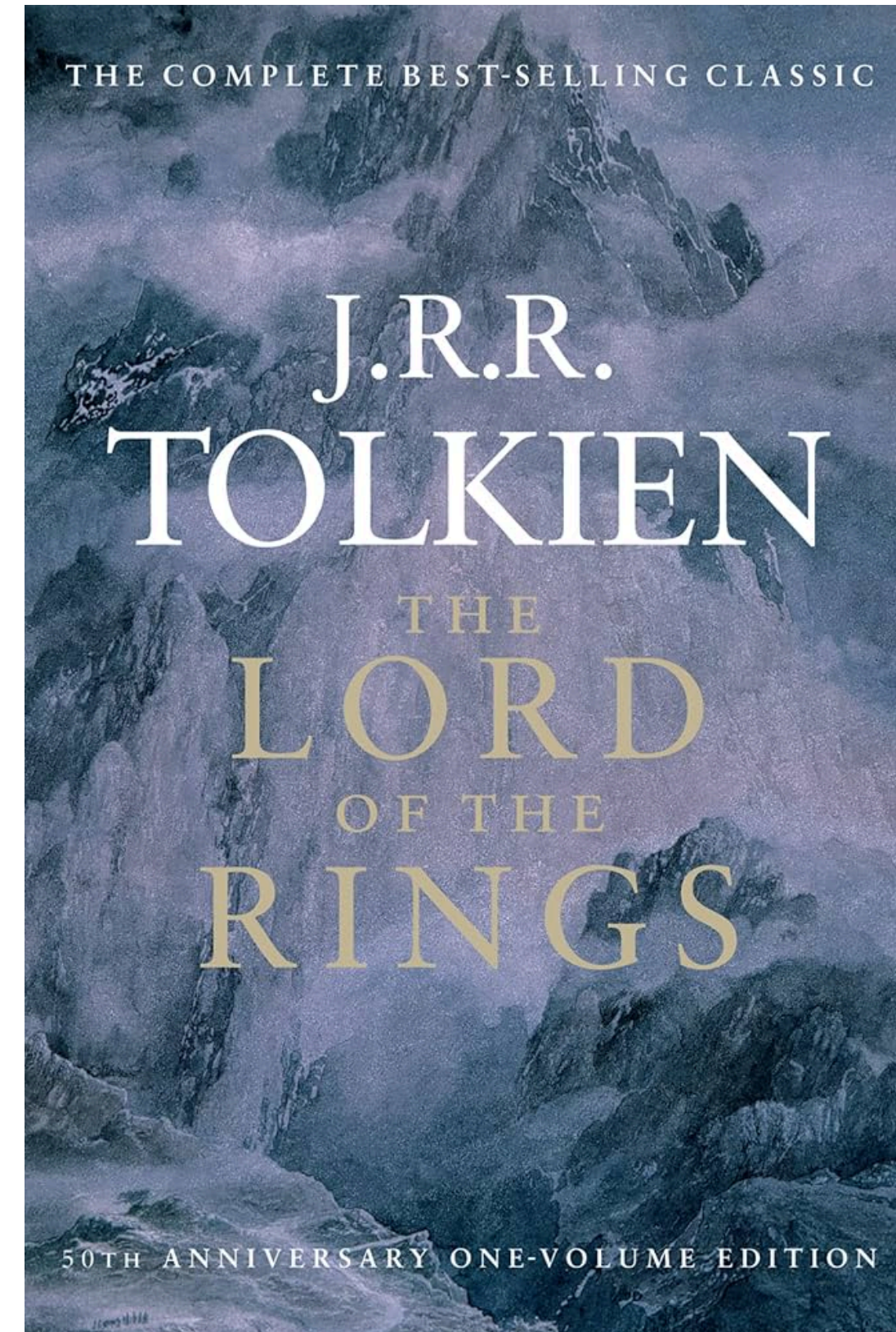
Advantages of nanopore sequencing

- 1) Long reads
- 2) Real-time sequencing
- 3) Portable sequencing
- 4) One platform, multiple omics
- 5) Direct measures
- 6) In silico target sequencing (adaptive sampling)



Let's try again

Reconstruct the text using longer
fragments

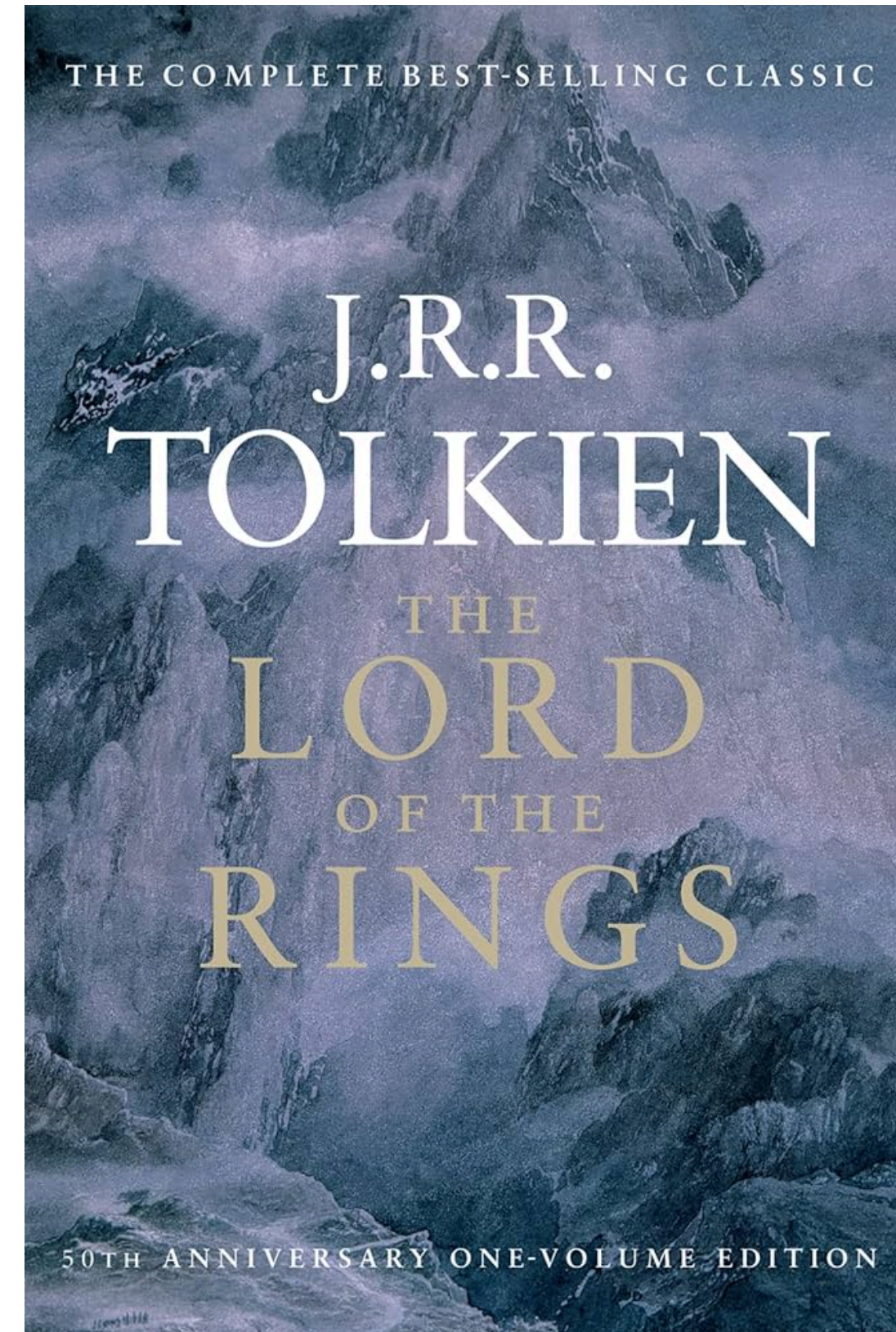




Let's try again

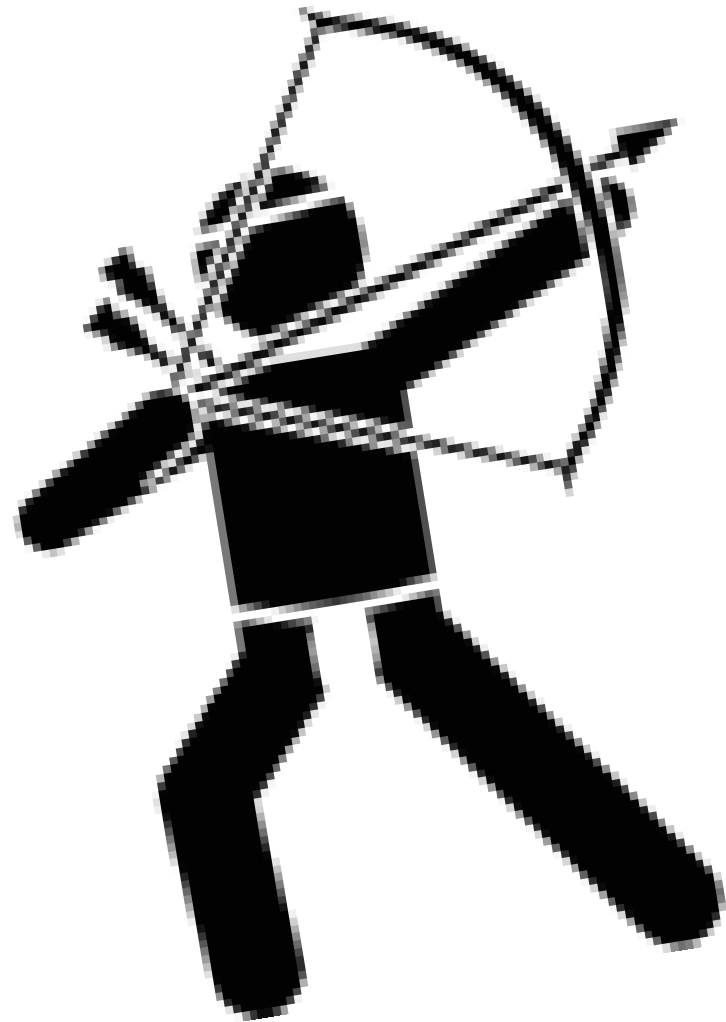
“When Mr. Bilbo Baggins of Bag End announced that he would shortly be celebrating his eleventy-first birthday with a party of special magnificence, there was much talk and excitement in Hobbiton.

Bilbo was very rich and very peculiar, and had been the wonder of the Shire for sixty years, ever since his remarkable disappearance and unexpected return. The riches he had brought back from his travels had now become a local legend, and it was popularly believed that the tunnels of Bag End were stuffed with treasures of all kinds.”



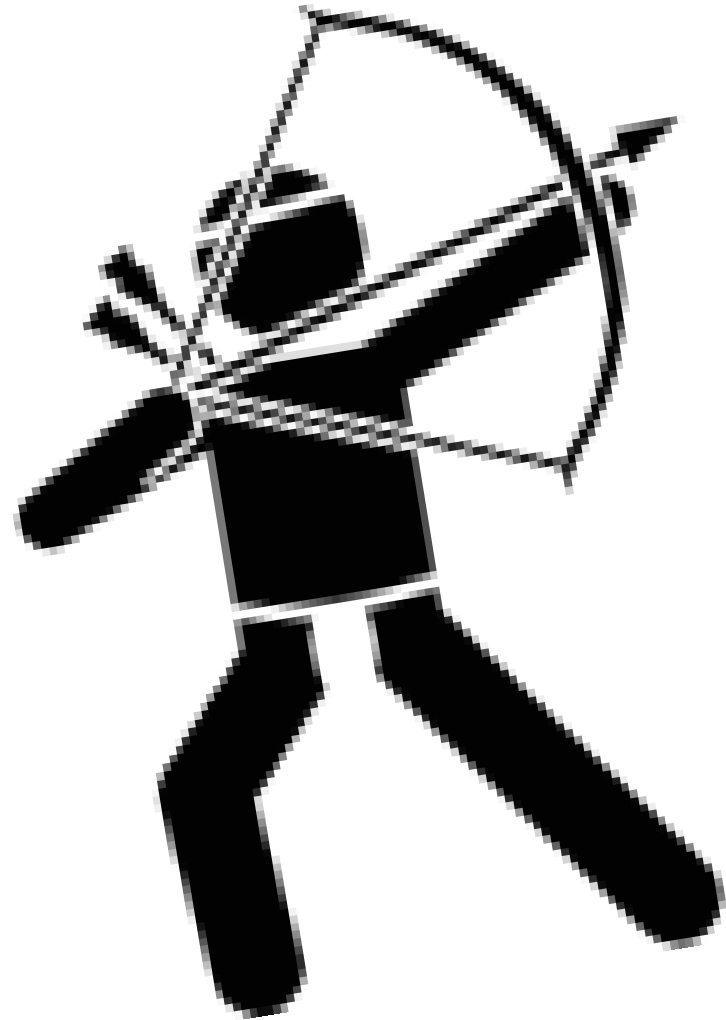


Target sequencing



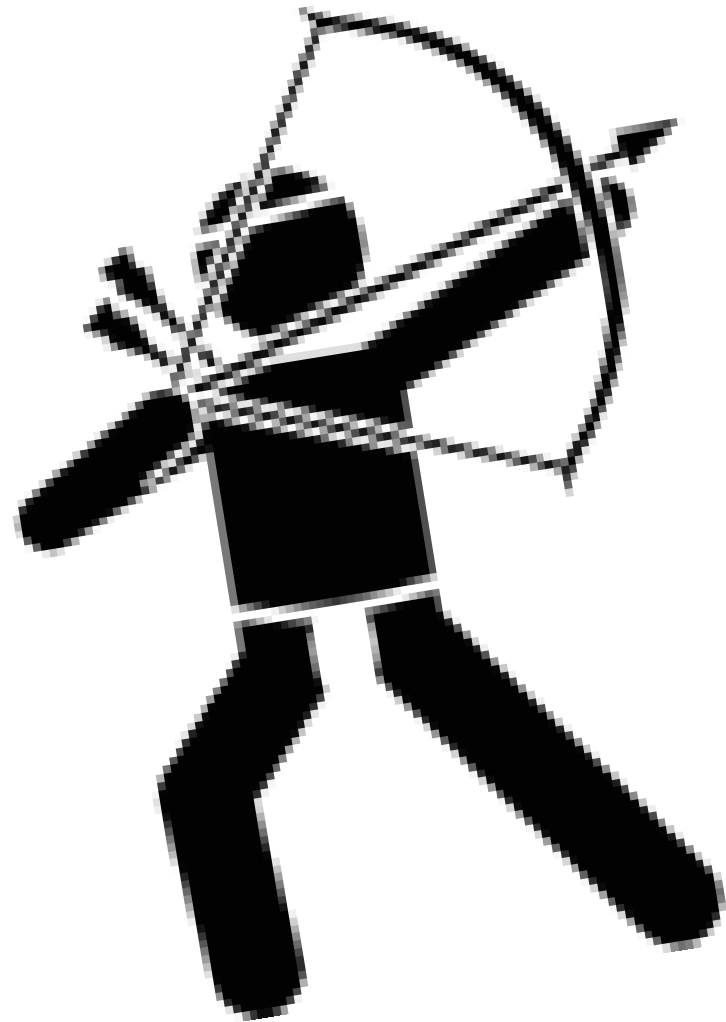


Target sequencing





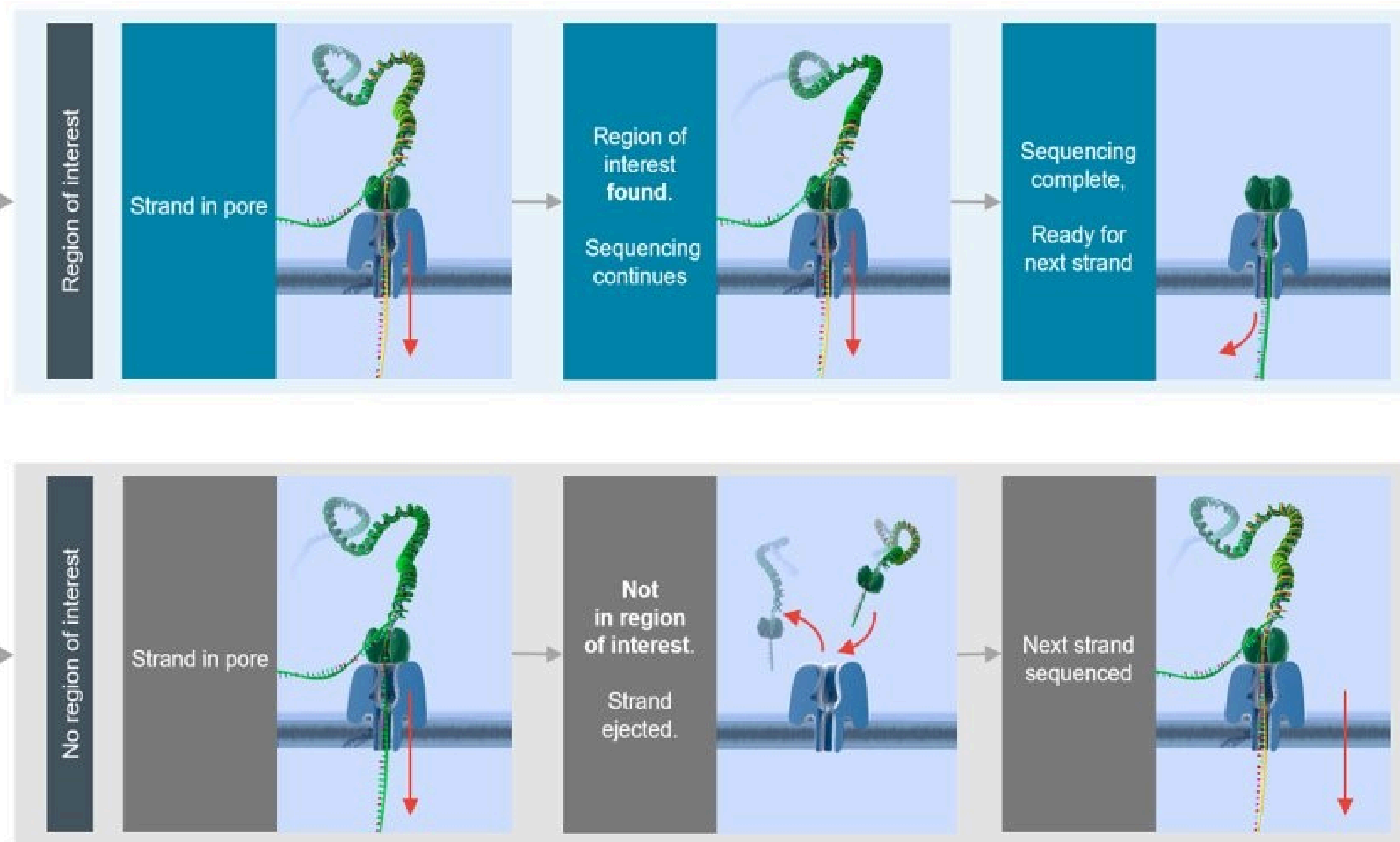
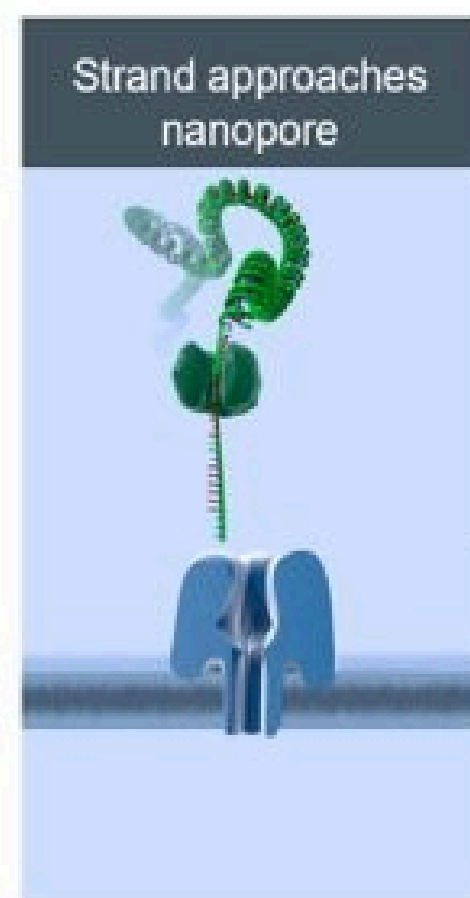
Target sequencing



Selecting and decoding specific portions of the genome
(e.g. a set of genes, a chromosome, the exome)



Adaptive sampling





Portable devices



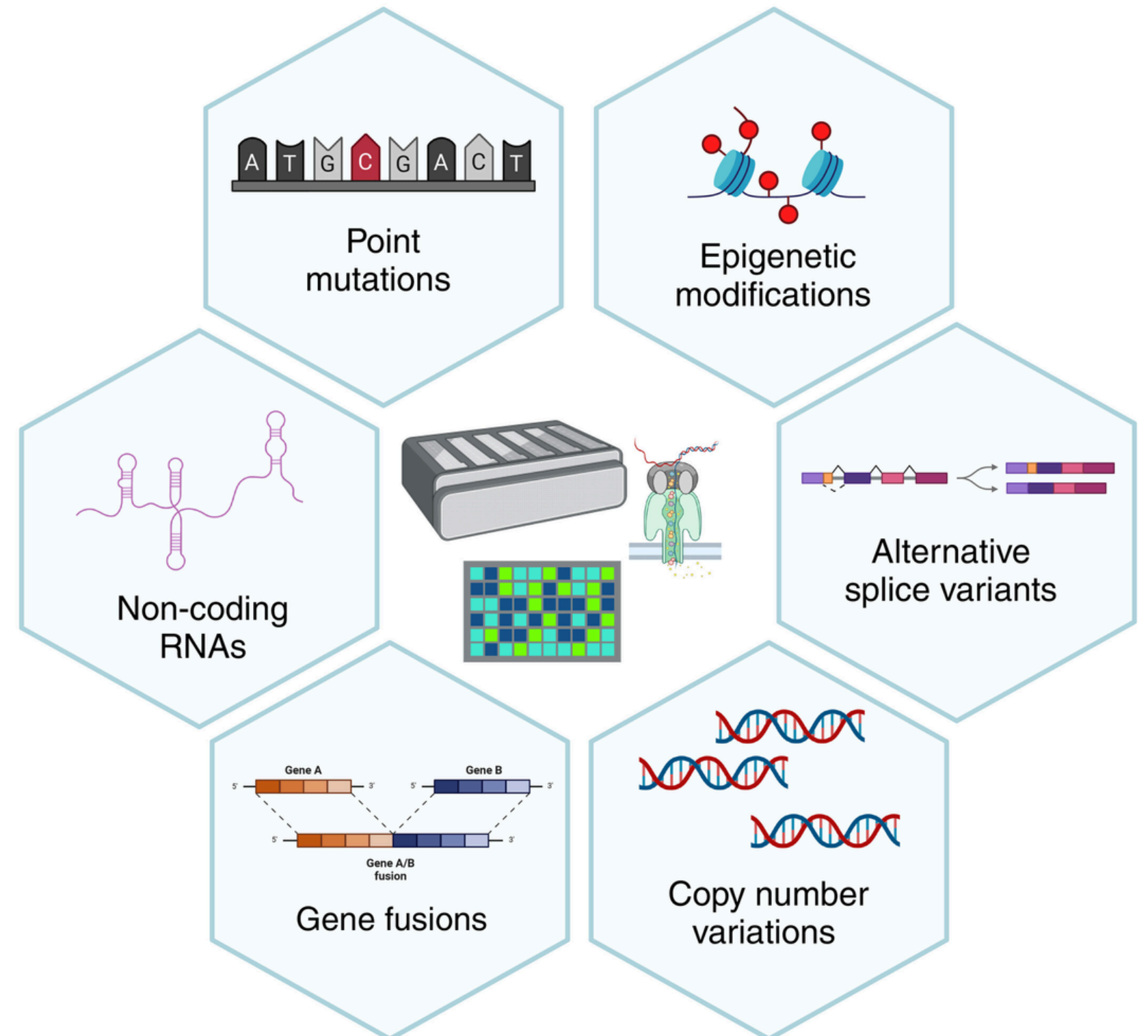
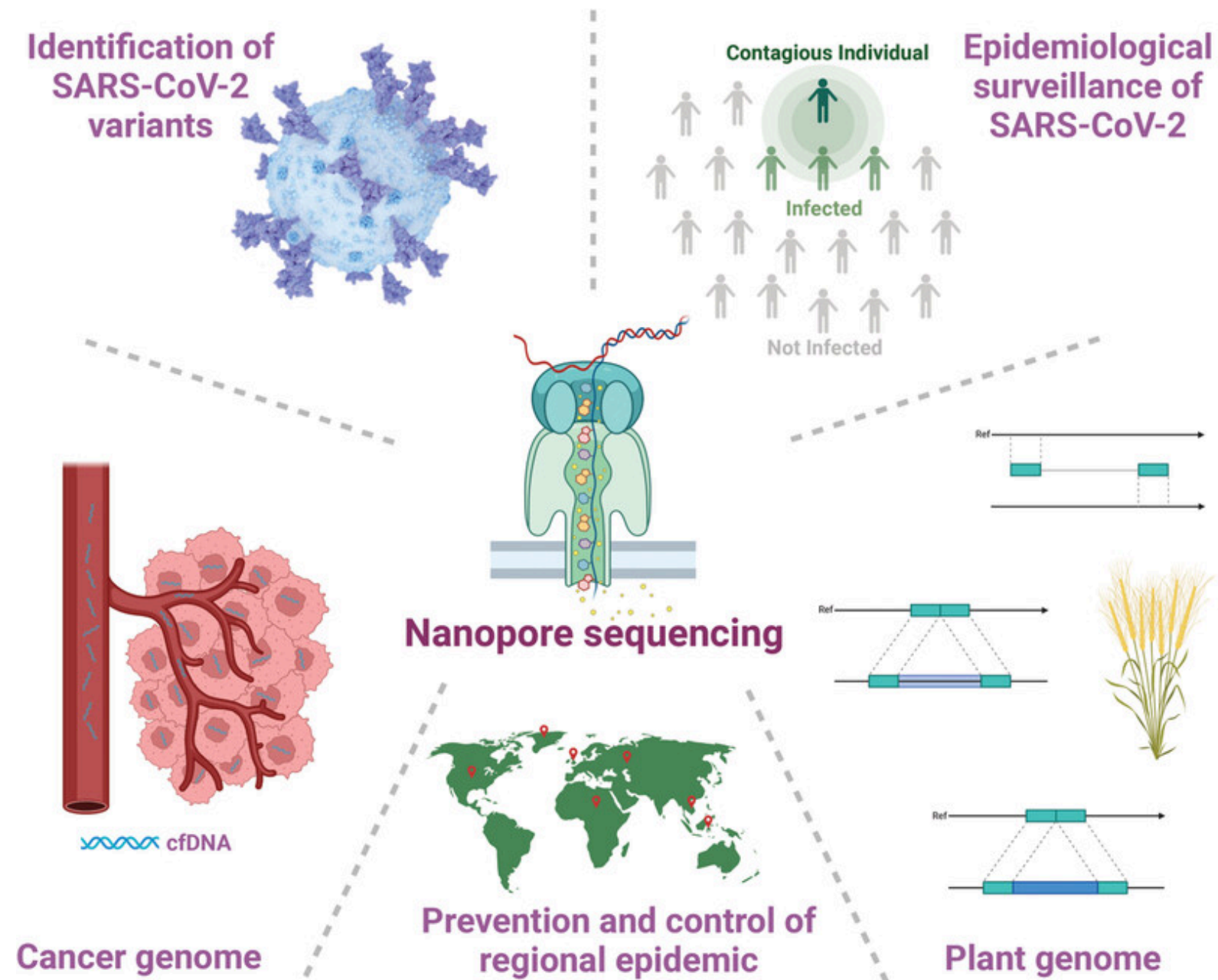


Portable devices



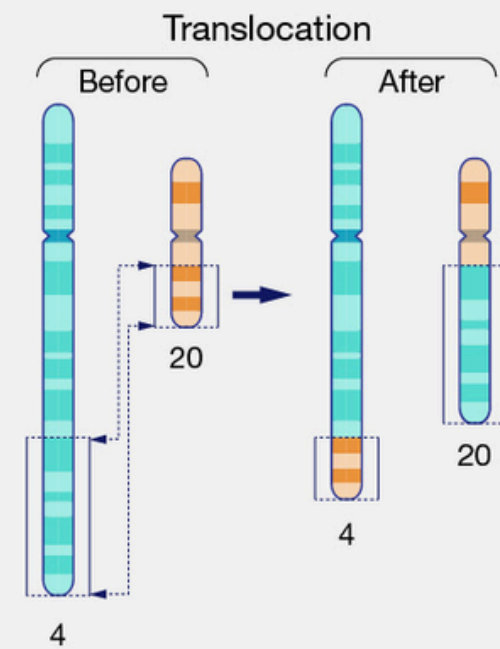
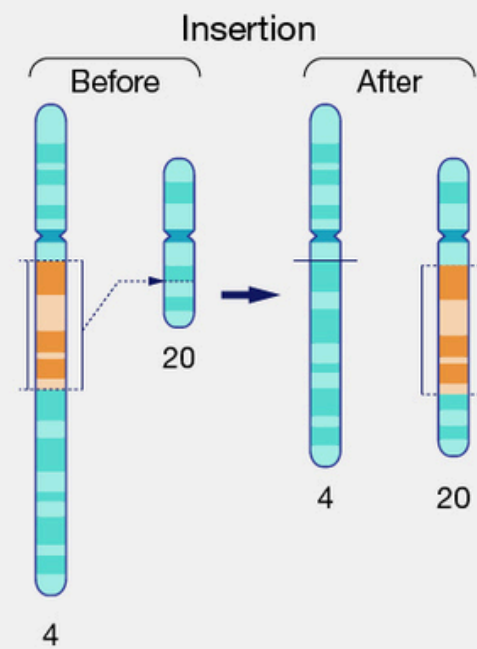
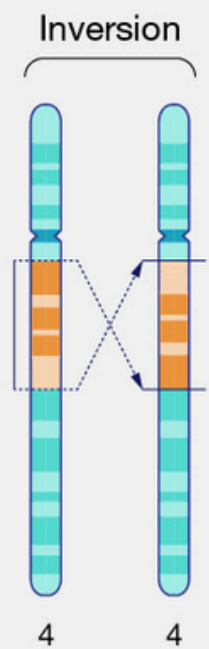
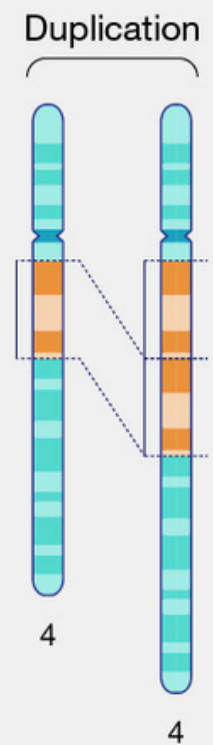
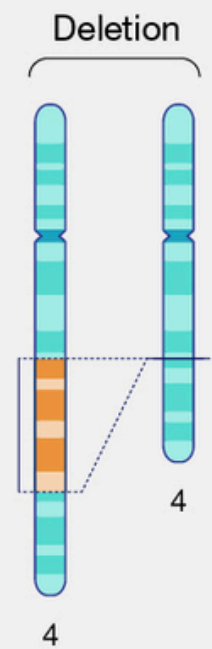


Applications of nanopore sequencing





Detection of complex structural variants





Characterization of tandem repeats

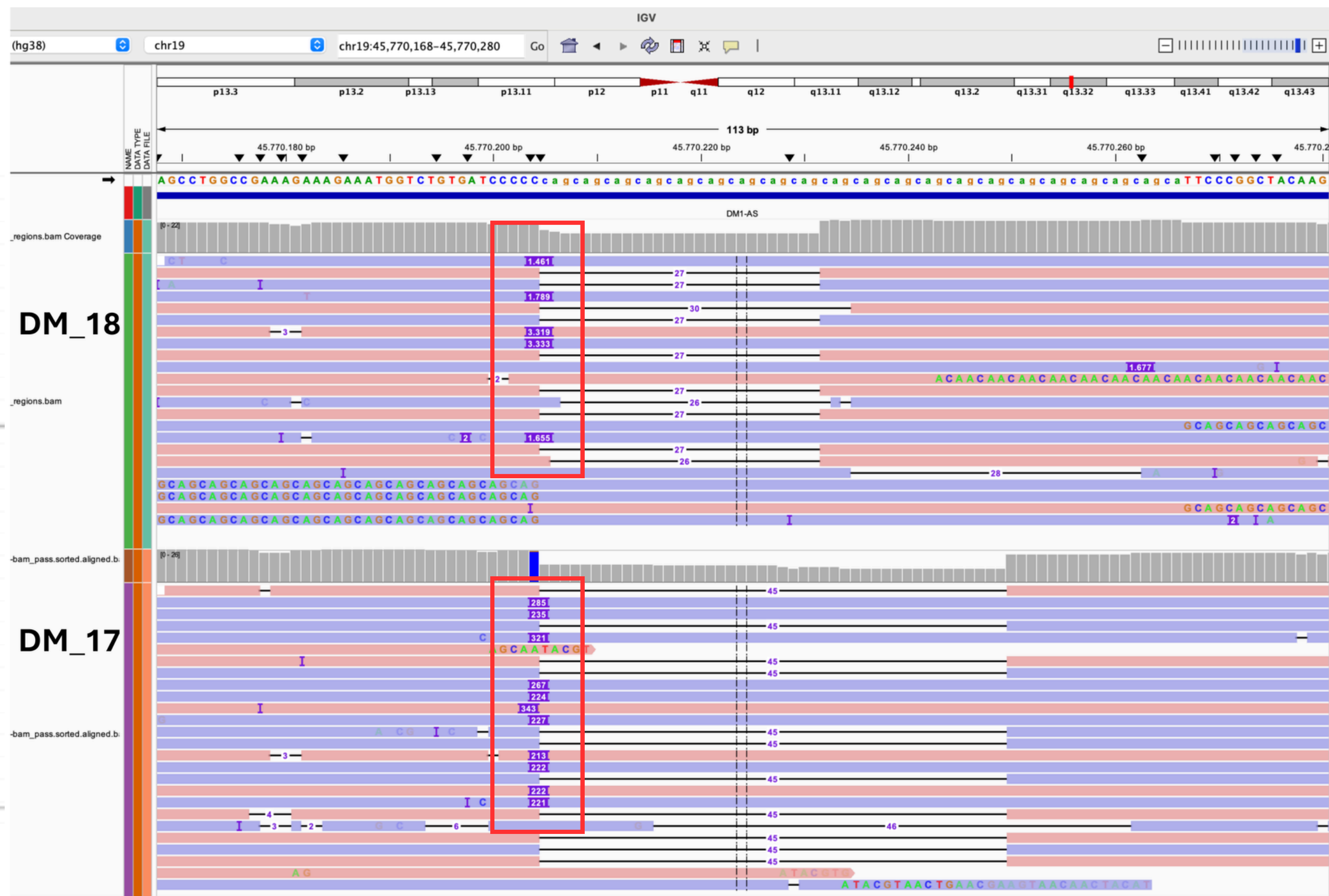
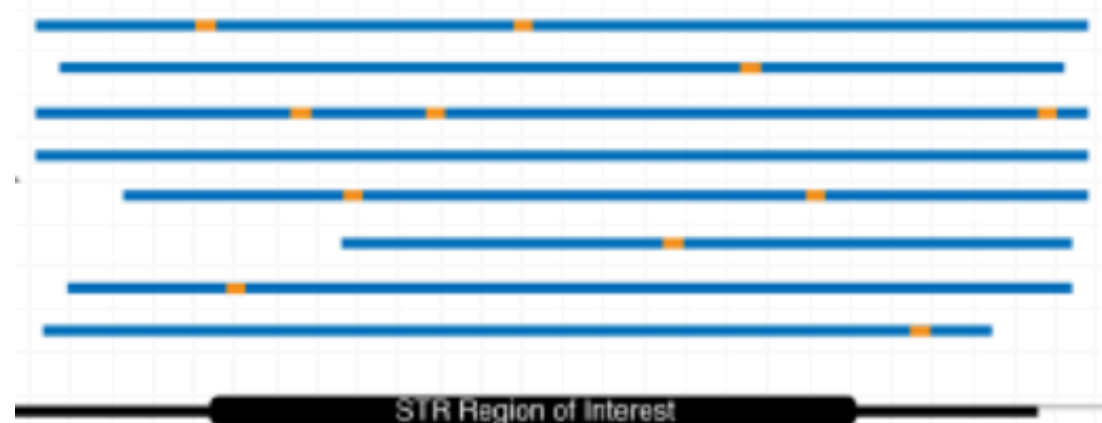
SHORT READS

Sequence data aligned to the genome. Short-reads are tiled together to estimate STR size.



NANOPORE LONG READS

Long-reads aligned to the genome. Reads cover the entire STR allowing accurate sizing. Random errors may be overcome with sufficient coverage over the region of interest.





Characterization of tandem repeats

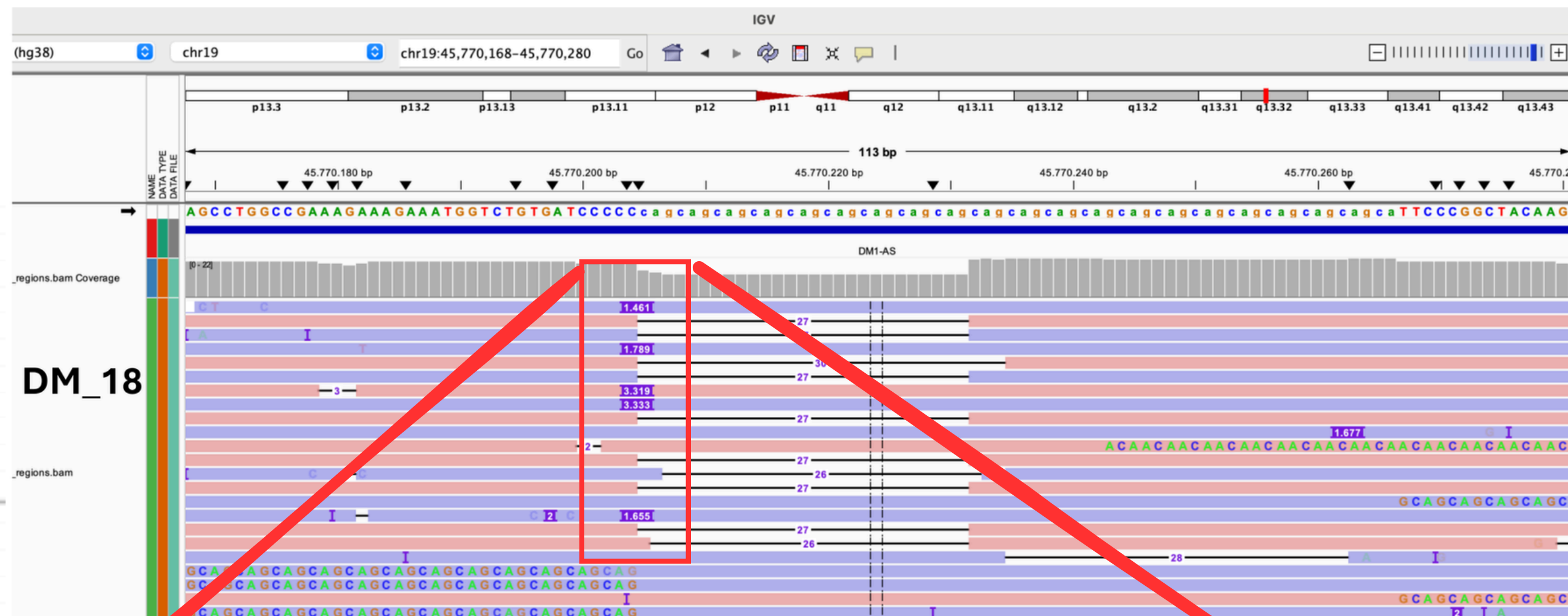
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Long-reads aligned to the genome. Reads cover the entire STR allowing accurate sizing. Random errors may be observed with sufficient coverage over the region of interest.



Expansion in DMPK (7b97eb27-ef56-413b-a422-ccce2abea0d3)

Total length: 1527 bp

888

456

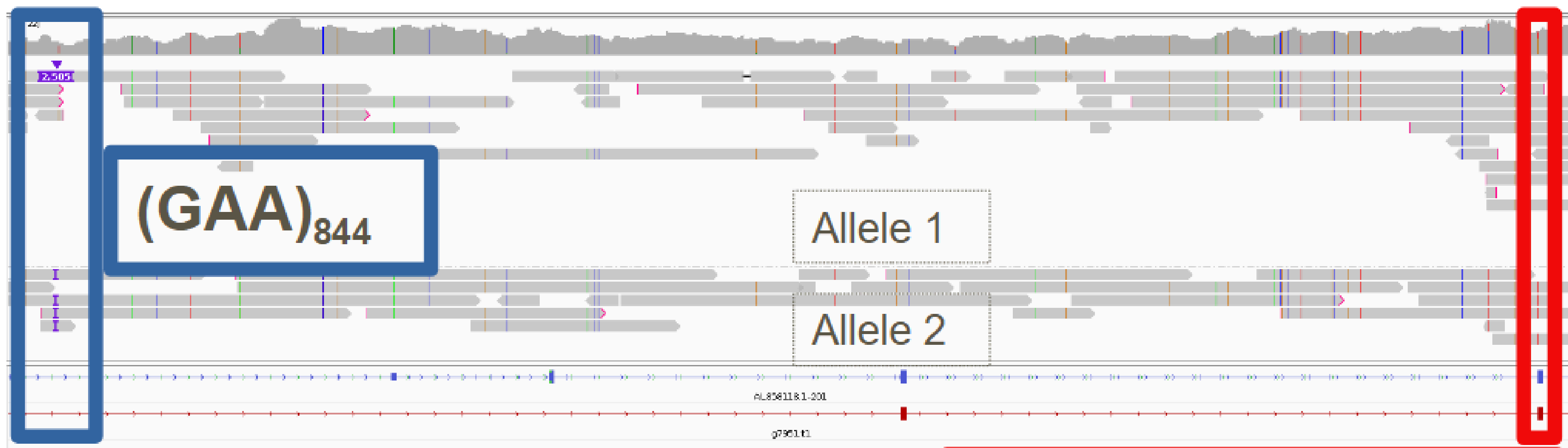
183

CTG
CTC
Other



Precise allele phasing

Assigning variants to the two homologous chromosomes



Allele 1: repeat expansion
Allele 2: pathogenic SNP

chr9:81238272



WE INTERRUPT THIS PROGRAM FOR A
COMMERCIAL BREAK



On a wonderful hill in Bologna..





On a wonderful hill in Bologna..





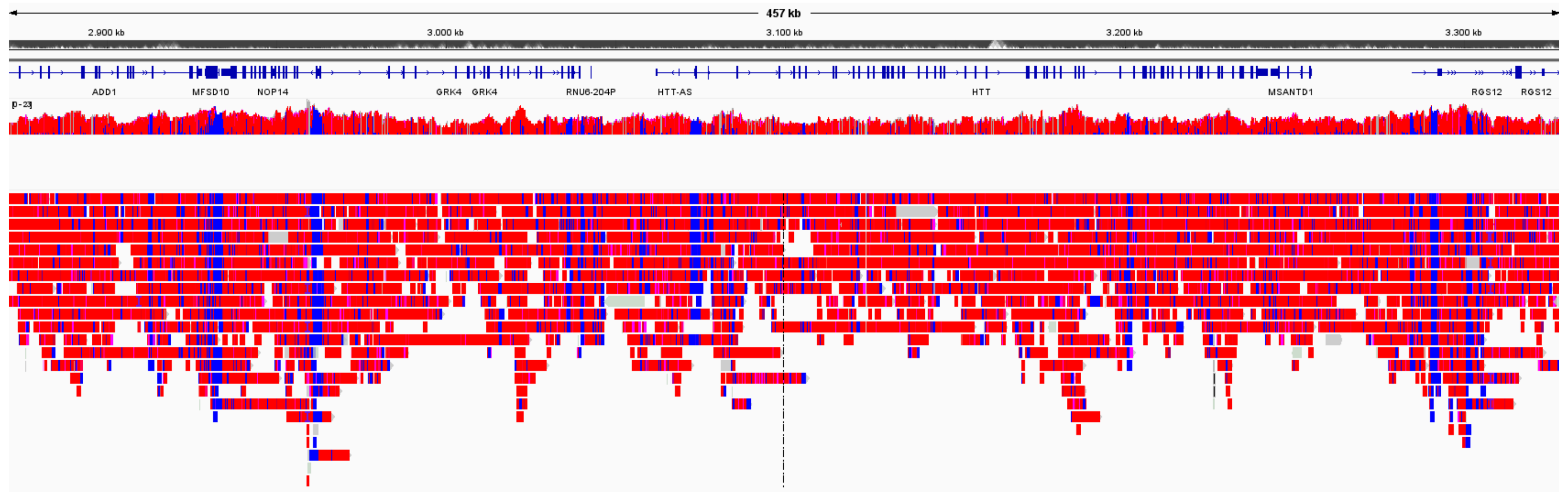
On a wonderful hill in Bologna..





Epigenetics

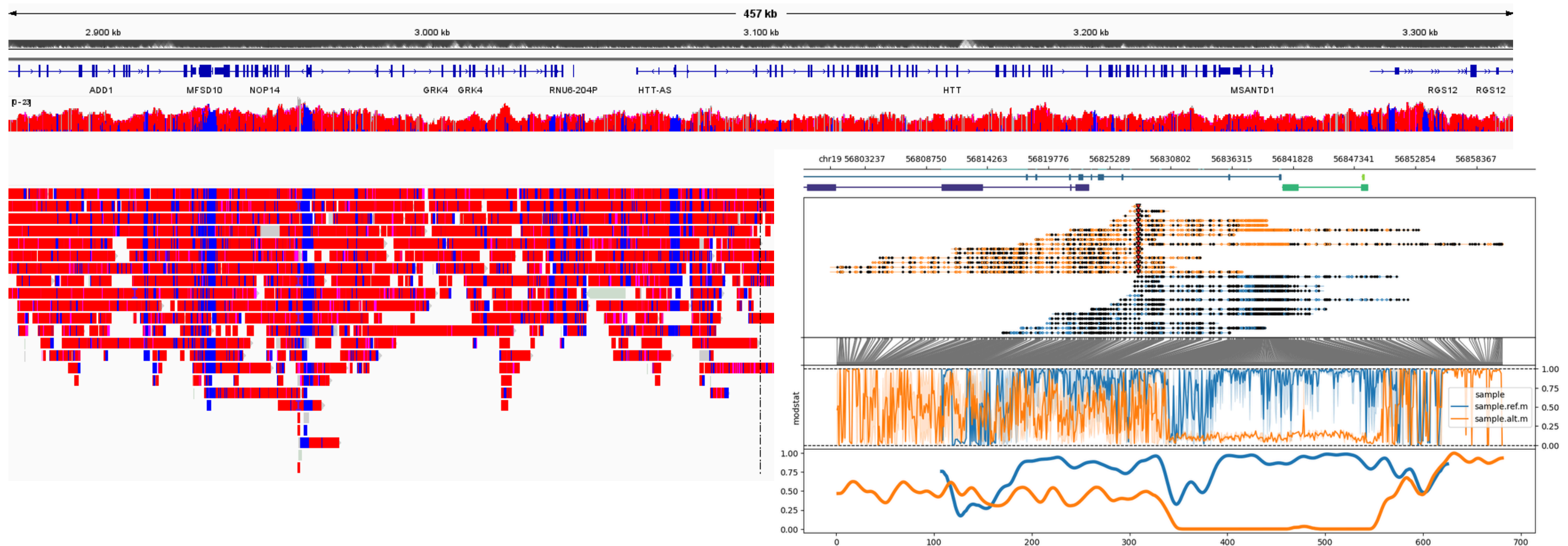
Nanopore sequencing allows to **directly detect** (without chemical preprocessing) **methylated bases**





Epigenetics

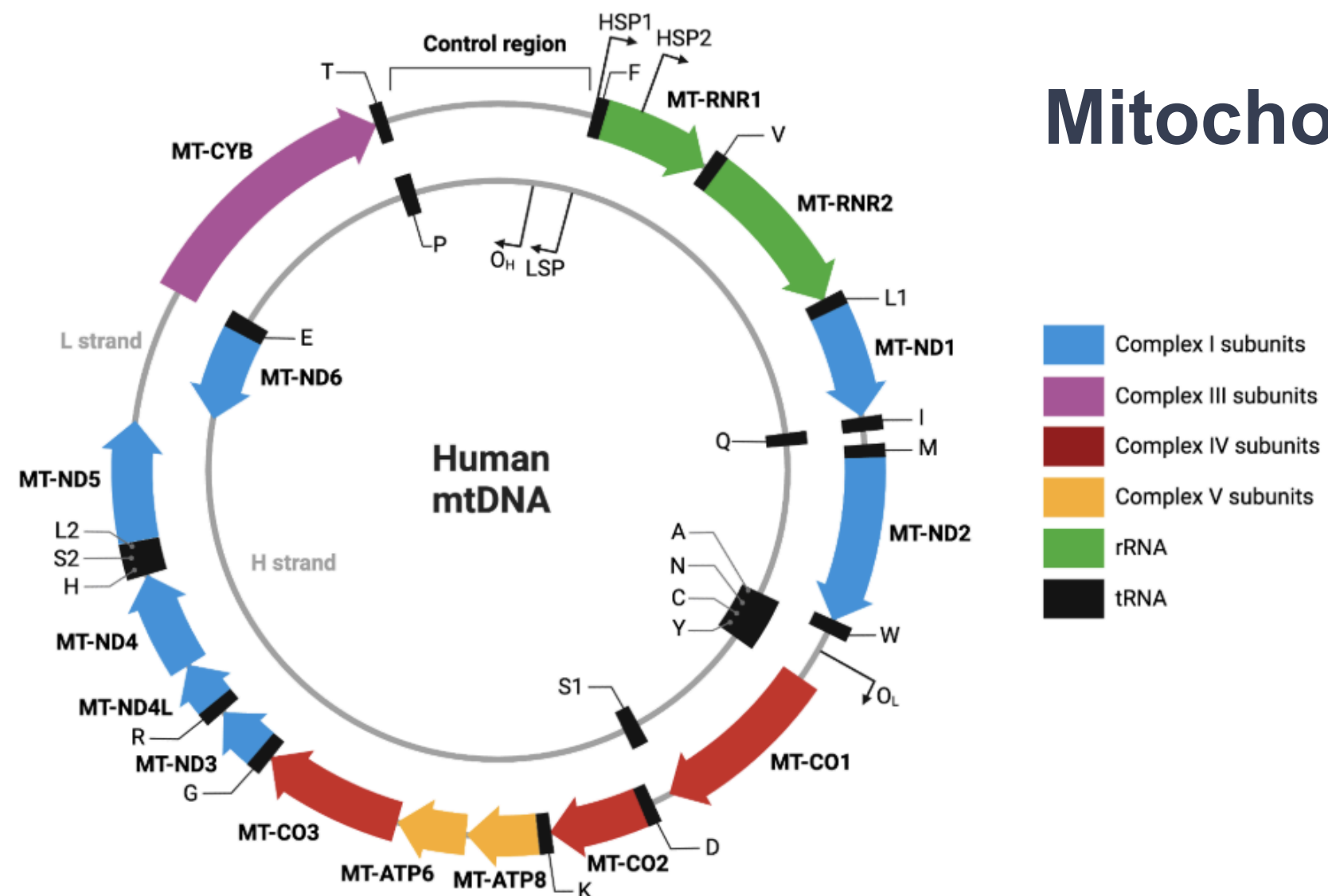
Nanopore sequencing allows to **directly detect** (without chemical preprocessing) **methyated bases**





Sequencing of mitochondrial DNA

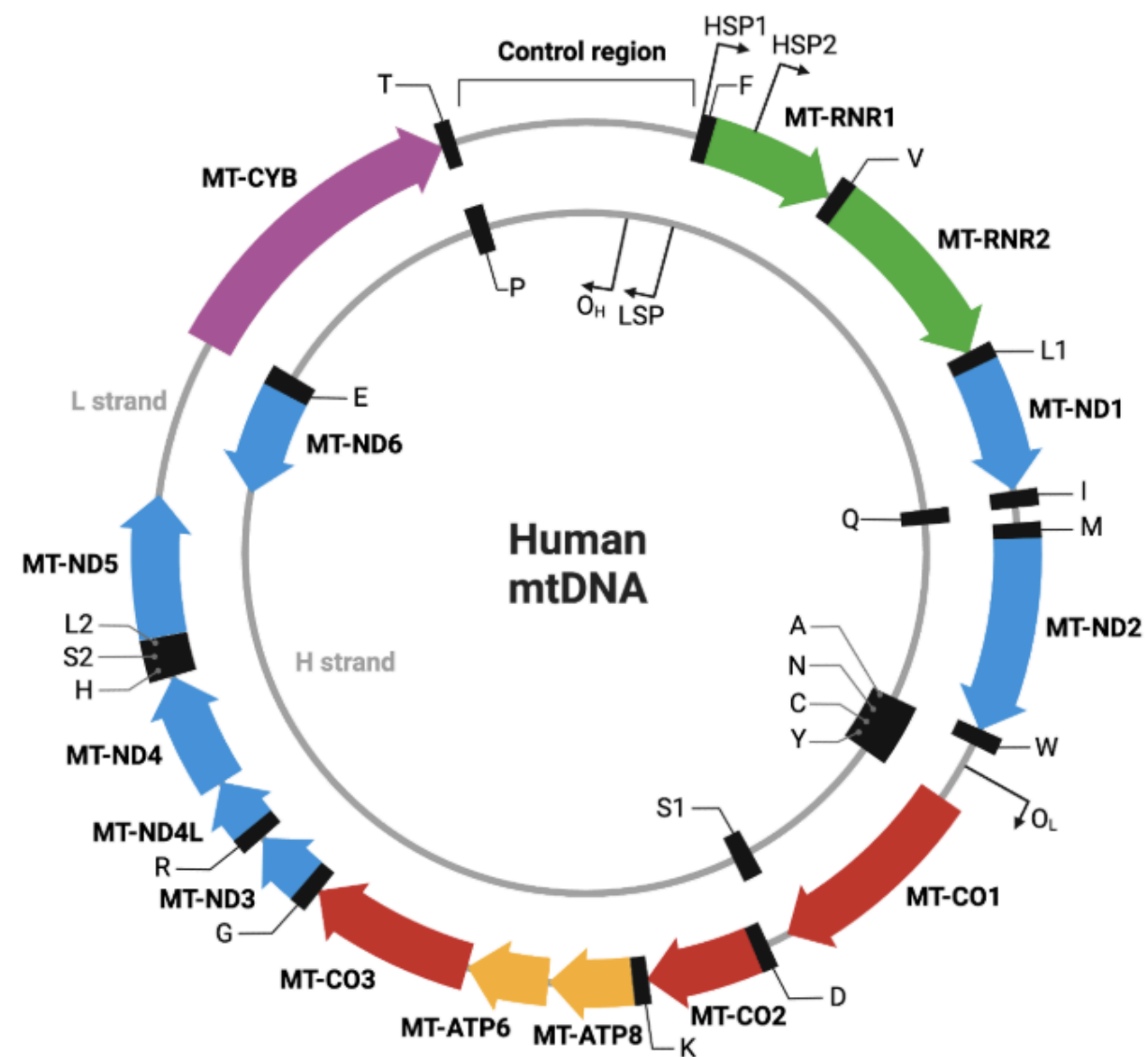
Mitochondrial DNA (mtDNA) is circular: problem of reconstruction and alignment





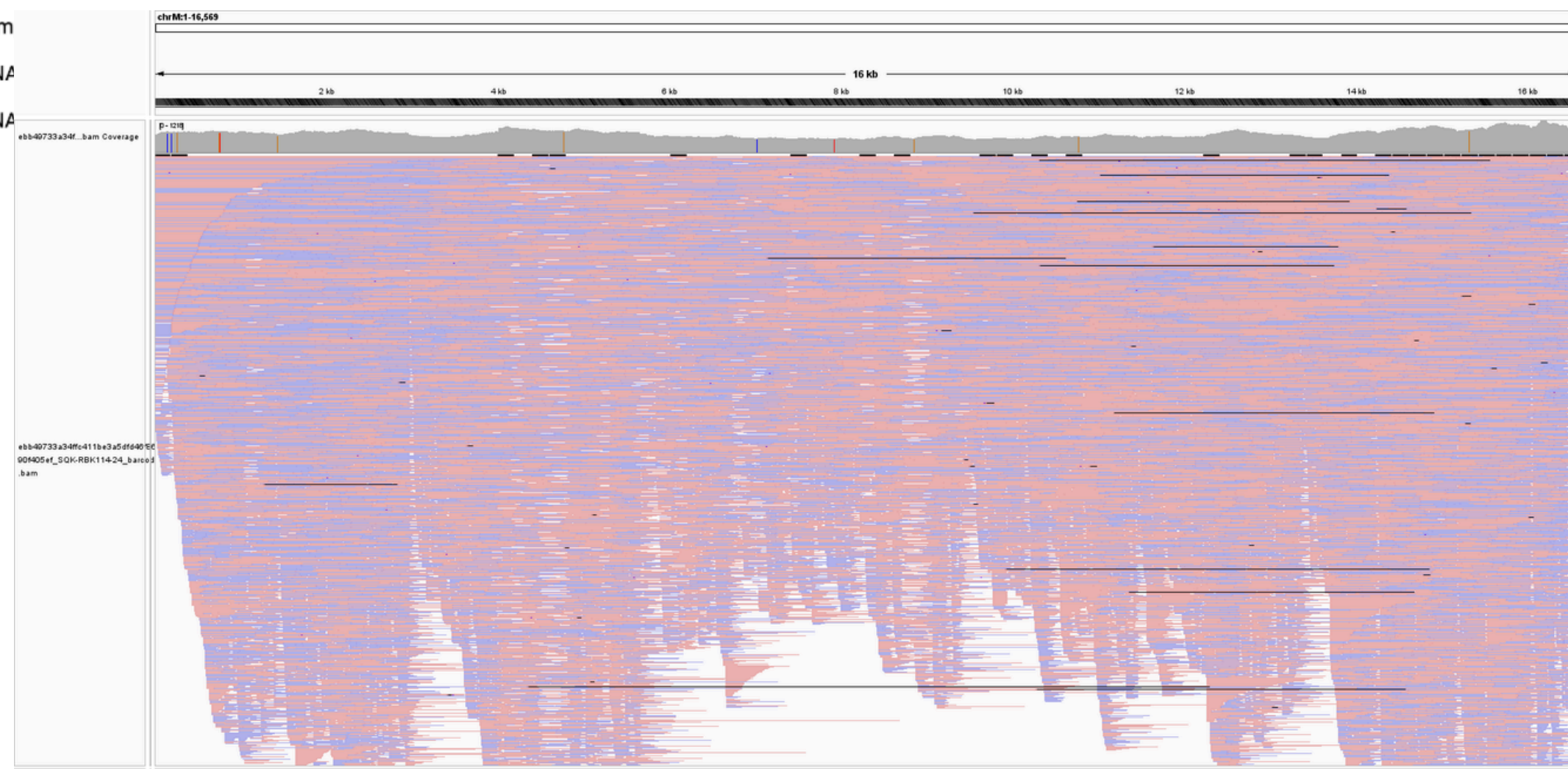
Sequencing of mitochondrial DNA

Mitochondrial DNA (mtDNA) is circular: problem of reconstruction and alignment



- Complex I subunits
- Complex III subunits
- Complex IV subunits
- Com
- rRNA
- tRNA

Nanopore allows to sequence an entire molecule of mtDNA





Complete sequence of human genome (2022)

SPECIAL SECTION

COMPLETING THE HUMAN GENOME

RESEARCH ARTICLE

HUMAN GENOMICS

The complete sequence of a human genome

Sergey Nurk¹†, Sergey Koren¹†, Arang Rhie¹†, Mikko Rautiainen¹†, Andrey V. Bzikadze², Alla Mikheenko³, Mitchell R. Vollger⁴, Nicolas Altemose⁵, Lev Uralsky^{6,7}, Ariel Gershman⁸, Sergey Aganezov⁹†, Savannah J. Hoyt¹⁰, Mark Diekhans¹¹, Glennis A. Logsdon⁴, Michael Alonge⁹, Stylianos E. Antonarakis¹², Matthew Borchers¹³, Gerard G. Bouffard¹⁴, Shelise Y. Brooks¹⁴, Gina V. Caldas¹⁵, Nae-Chyun Chen⁹, Haoyu Cheng^{16,17}, Chen-Shan Chin¹⁸, William Chow¹⁹, Leonardo G. de Lima¹³, Philip C. Dishuck⁴, Richard Durbin^{19,20}, Tatiana Dvorkina³, Ian T. Fiddes²¹, Giulio Formenti^{22,23}, Robert S. Fulton²⁴, Arkarachai Fungtammasan¹⁸, Erik Garrison^{11,25}, Patrick G. S. Grady¹⁰, Tina A. Graves-Lindsay²⁶, Ira M. Hall²⁷, Nancy F. Hansen²⁸, Gabrielle A. Hartley¹⁰, Marina Haukness¹¹, Kerstin Howe¹⁹, Michael W. Hunkapiller²⁹, Chirag Jain^{1,30}, Miten Jain¹¹, Erich D. Jarvis^{22,23}, Peter Kerpedjiev³¹, Melanie Kirsche⁹, Mikhail Kolmogorov³², Jonas Koriach²⁹, Milinn Kremitzki²⁶, Heng Li^{16,17}, Valerie V. Maduro³³, Tobias Marschall³⁴, Ann M. McCartney¹, Jennifer McDaniel³⁵, Danny E. Miller^{4,36}, James C. Mullikin^{14,28}, Eugene W. Myers³⁷, Nathan D. Olson³⁵, Benedict Paten¹¹, Paul Peluso²⁹, Pavel A. Pevzner³², David Porubsky⁴, Tamara Potapova¹³, Evgeny I. Rogae^{6,7,38,39}, Jeffrey A. Rosenfeld⁴⁰, Steven L. Salzberg^{9,41}, Valerie A. Schneider⁴², Fritz J. Sedlazeck⁴³, Kishwar Shafin¹¹, Colin J. Shew⁴⁴, Alaina Shumate⁴¹, Ying Sims¹⁹, Arian F. A. Smit⁴⁵, Daniela C. Soto⁴⁴, Ivan Sovic^{29,46}, Jessica M. Storer⁴⁵, Aaron Streets^{5,47}, Beth A. Sullivan⁴⁸, Françoise Thibaud-Nissen⁴², James Torrance¹⁹, Justin Wagner³⁵, Brian P. Walenz¹, Aaron Wenger²⁹, Jonathan M. D. Wood¹⁹, Chunlin Xiao⁴², Stephanie M. Yan⁴⁹, Alice C. Young¹⁴, Samantha Zarate⁹, Urvashi Surti⁵⁰, Rajiv C. McCoy⁴⁹, Megan Y. Dennis⁴⁴, Ivan A. Alexandrov^{3,7,51}, Jennifer L. Gerton^{13,52}, Rachel J. O'Neill¹⁰, Winston Timp^{8,41}, Justin M. Zook³⁵, Michael C. Schatz^{9,49}, Evan E. Eichler^{4,53*}, Karen H. Miga^{11,54*}, Adam M. Phillippy^{1*}

Since its initial release in 2000, the human reference genome has covered only the euchromatic fraction of the genome, leaving important heterochromatic regions unfinished. Addressing the remaining 8% of the genome, the Telomere-to-Telomere (T2T) Consortium presents a complete 3.055 billion–base pair sequence of a human genome, T2T-CHM13, that includes gapless assemblies for all chromosomes except Y, corrects errors in the prior references, and introduces nearly 200 million base pairs of sequence containing 1956 gene predictions, 99 of which are predicted to be protein coding. The completed regions include all centromeric satellite arrays, recent segmental duplications, and the short arms of all five acrocentric chromosomes, unlocking these complex regions of the genome to variational and functional studies.

The current human reference genome was released by the Genome Reference Consortium (GRC) in 2013 and most recently patched in 2019 (GRCh38.p13) (*1*). This reference traces its origin to the publicly

funded Human Genome Project (*2*) and has been continually improved over the past two decades. Unlike the competing Celera effort (*3*) and most modern sequencing projects based on “shotgun” sequence assembly (*4*),

the GRC assembly was constructed from sequenced bacterial artificial chromosomes (BACs) that were ordered and oriented along the human genome by means of radiation hybrid, genetic linkage, and fingerprint maps. However, limitations of BAC cloning led to an underrepresentation of repetitive sequences, and the opportunistic assembly of BACs derived from multiple individuals resulted in a mosaic of haplotypes. As a result, several GRC assembly gaps are unsolvable because of incompatible structural polymorphisms on their flanks, and many other repetitive and polymorphic regions were left unfinished or incorrectly assembled (*5*).

The GRCh38 reference assembly contains 151 mega–base pairs (Mbp) of unknown sequence distributed throughout the genome, including pericentromeric and subtelomeric regions, recent segmental duplications, ampliconic gene arrays, and ribosomal DNA (rDNA) arrays, all of which are necessary for fundamental cellular processes (Fig. 1A). Some of the largest reference gaps include human satellite (HSat) repeat arrays and the short arms of all five acrocentric chromosomes, which are represented in GRCh38 as multimegabase stretches of unknown bases (Fig. 1, B and C). In addition to these apparent gaps, other regions of GRCh38 are artificial or are otherwise incorrect. For example, the centromeric alpha satellite arrays are represented as computationally generated models of alpha satellite monomers to serve as decoys for resequencing analyses (*6*), and sequence assigned to the short arm of chromosome 21 appears falsely duplicated and poorly assembled (*7*). When compared with other human genomes, GRCh38 also shows a genome-wide deletion bias that is indicative of incomplete assembly (*8*). Despite finishing efforts from both the Human Genome Project (*9*) and GRC (*1*) that improved the quality of the reference, there was limited



Infectious diseases

- Rapid identification of pathogens



Infectious diseases

- Rapid identification of pathogens
- Epidemic tracking (**Ebola in West Africa**)

SCIENCE

Fighting Ebola With a Palm-Sized DNA Sequencer

The MinION, a pocket-sized, USB-powered sequencing machine, lets scientists track the spread of deadly diseases in real-time.

By Ed Yong



Raymond Koundouno using a MinION. (Sophie DuraEffour)



Infectious diseases

- Rapid identification of pathogens
- Epidemic tracking (**Ebola in West Africa**)
- Crucial role during **SARS-CoV-2** pandemic

SCIENCE

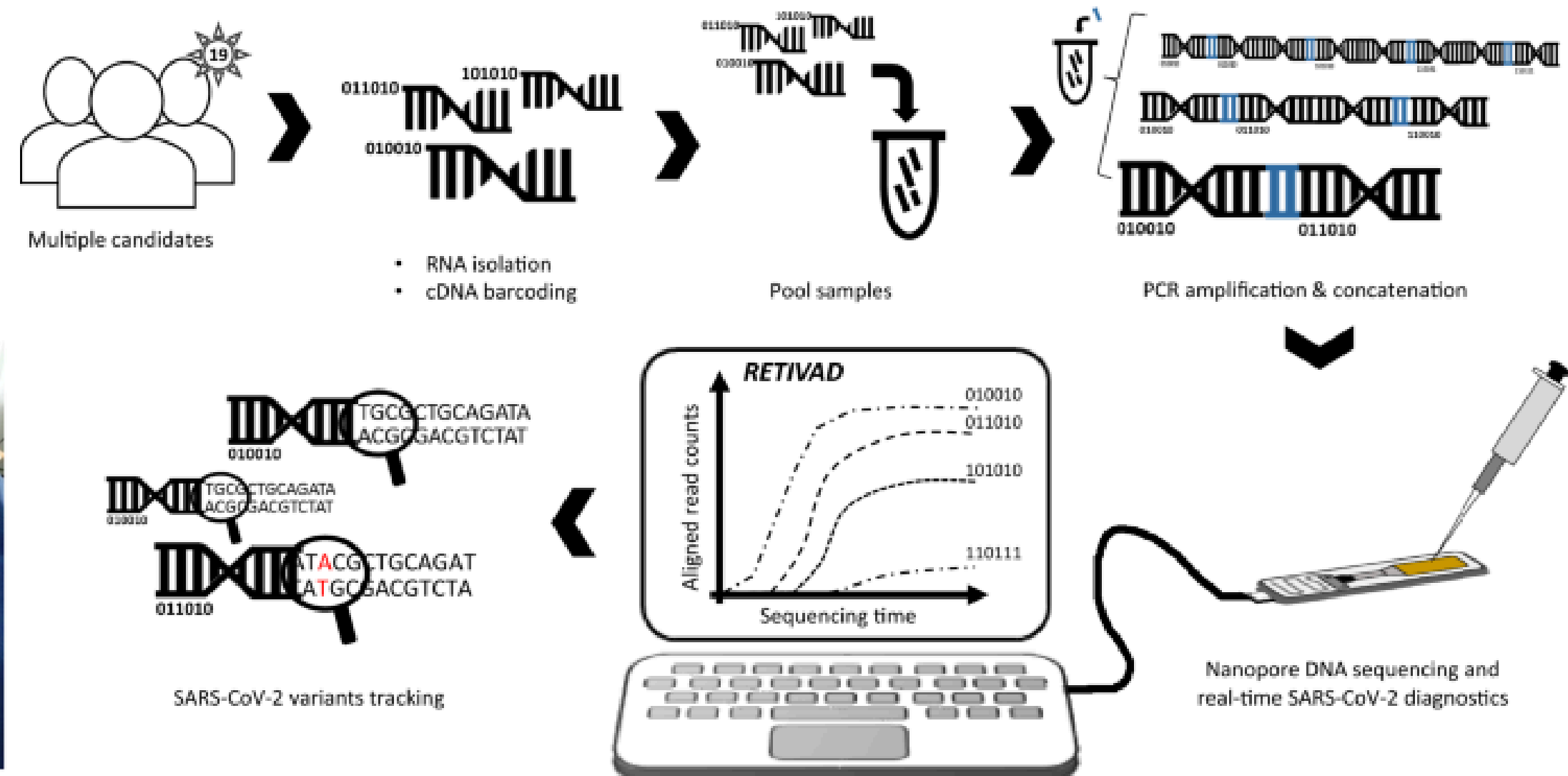
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Metagenomics

- Analysis of microbial communities



environments



Article

Nanopore Sequencing Reveals Microbial Community Compositions on Microplastic in the Setun River of the Moscow Region

Andrey Eremin ^{1,2,*} , Vadim Trefilov ¹, Vladimir Rodin ¹, Alexander Sergeev ¹ , Anastasia Lisina ^{3,4},
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and Maria Zvereva ¹ 



Metagenomics

- Analysis of microbial communities
- Bacterial **antimicrobial resistance** surveillance

npj | antimicrobials & resistance

Review



<https://doi.org/10.1038/s44259-025-00157-5>

The applications and advantages of nanopore sequencing in bacterial antimicrobial resistance surveillance and research



environments



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Metagenomics

- Analysis of microbial communities
- Bacterial **antimicrobial resistance** surveillance
- Identification of **microbial species** in complex samples (water, soil, human microbiome)

npj | antimicrobials & resistance

Review



<https://doi.org/10.1038/s44259-025-00157-5>

The applications and advantages of nanopore sequencing in bacterial antimicrobial resistance surveillance and research



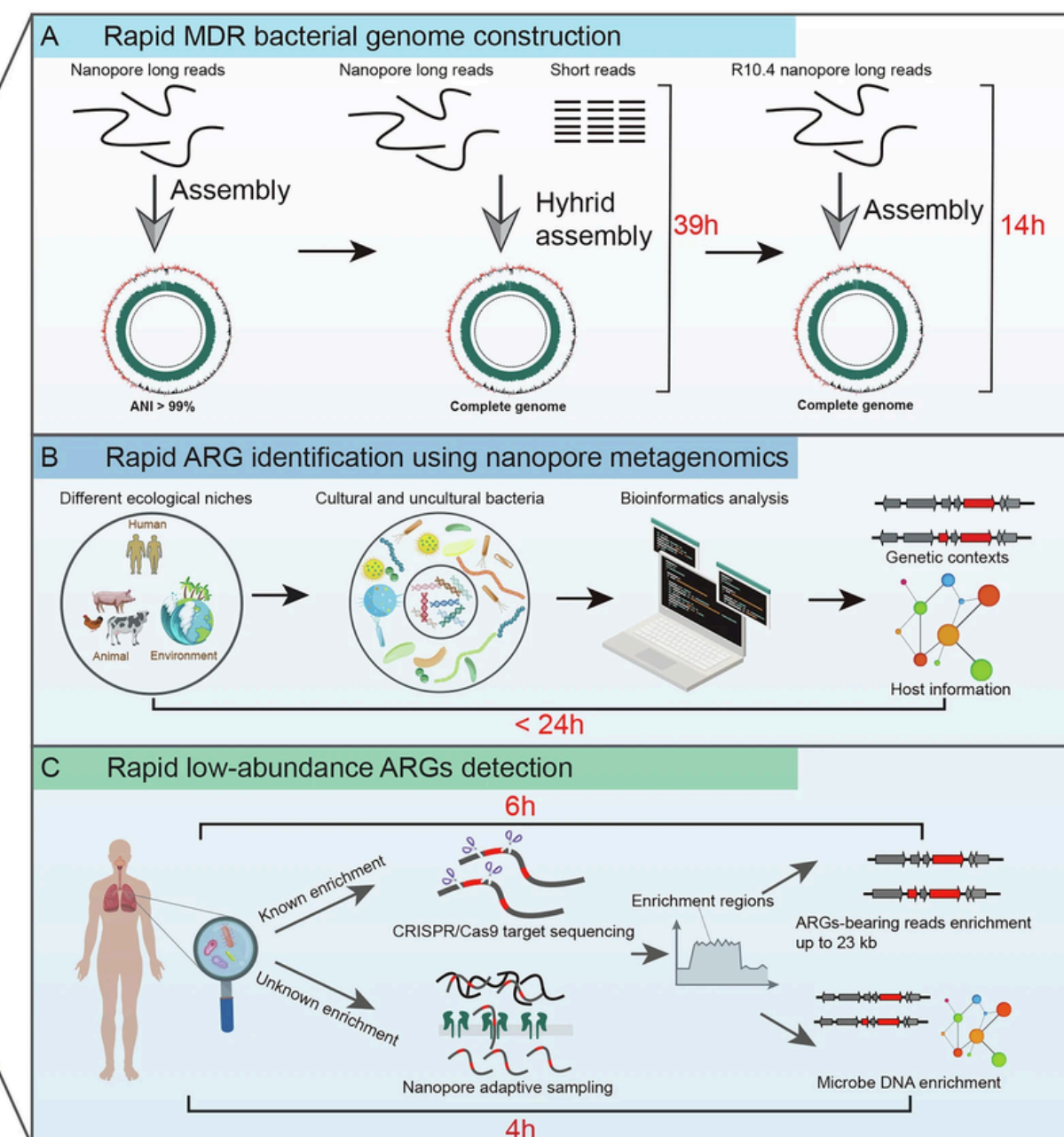
environments



Article

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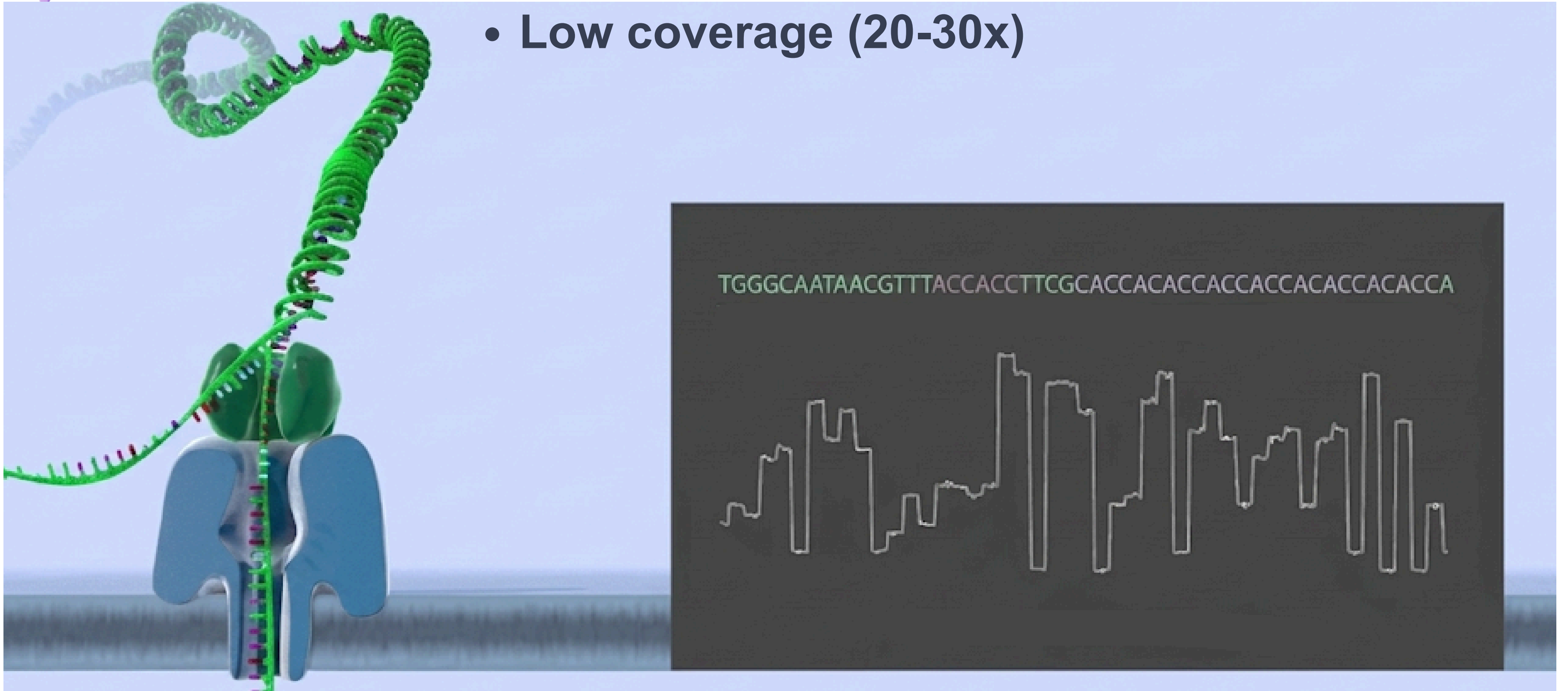
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Limitations of nanopore sequencing

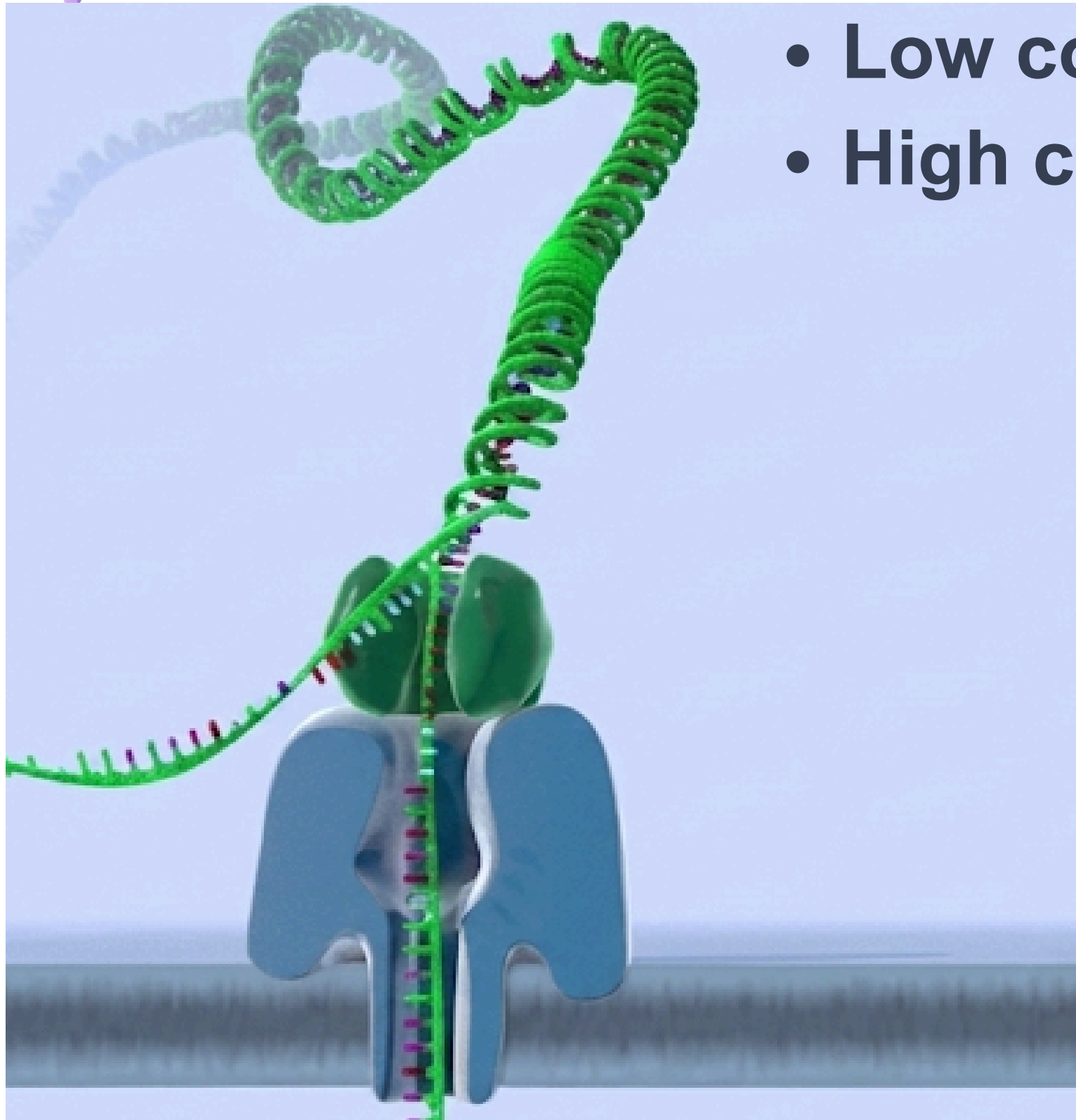
- Low coverage (20-30x)



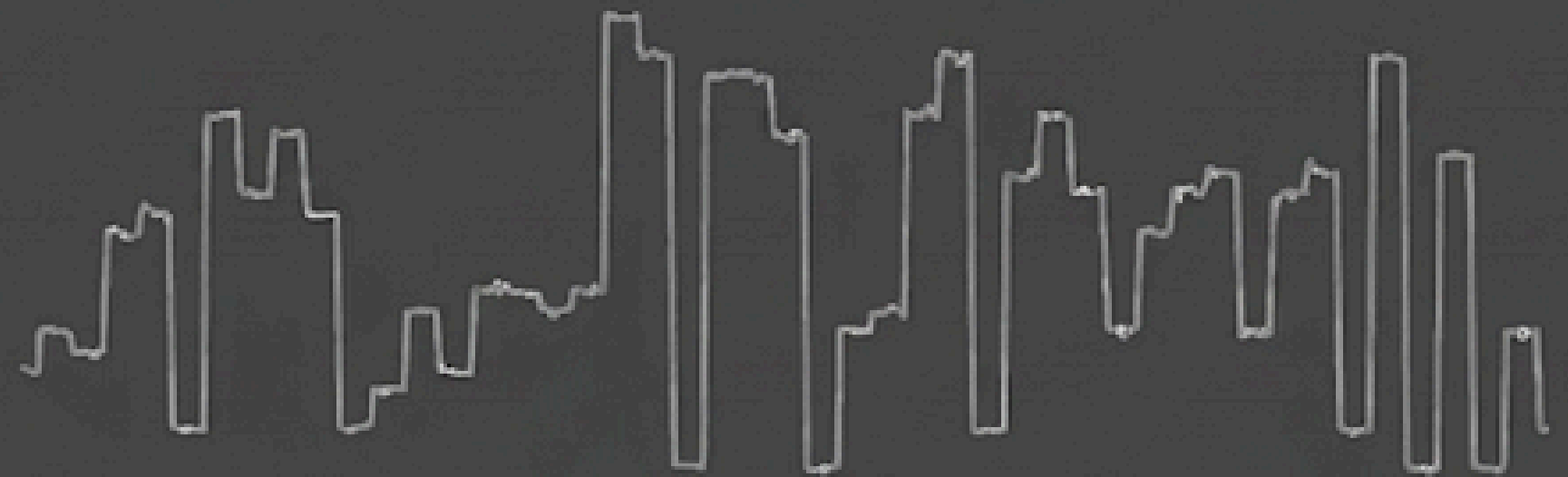


Limitations of nanopore sequencing

- Low coverage (20-30x)
- High costs (700-1000 € per run)



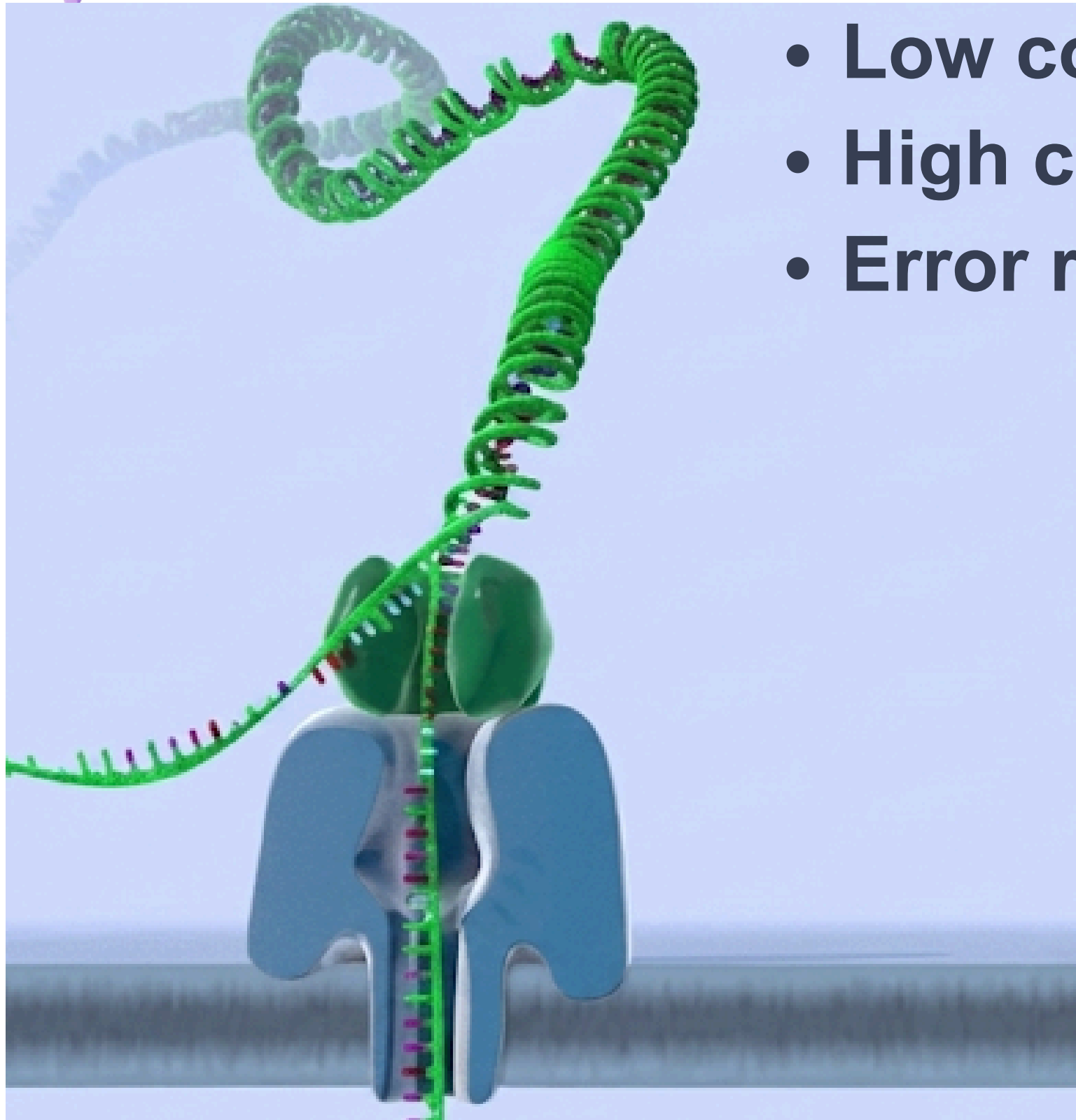
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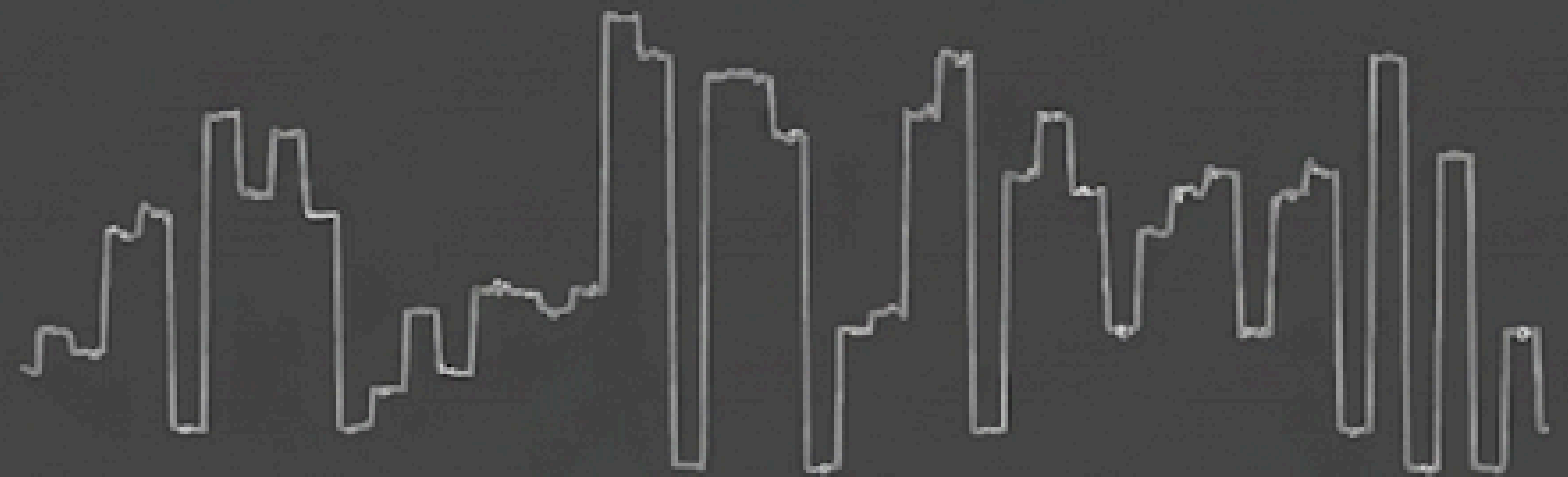


Limitations of nanopore sequencing

- Low coverage (20-30x)
- High costs (700-1000 € per run)
- Error rate (Q20 on average)



TGGGCAATAACGTTTACCACCTTCGCACCACACCACCACACCACACCA





Nature method of the year 2022





Conclusion

Nanopore sequencing **is redefining the boundaries** of diagnostics, epidemiological surveillance, and synthetic biology.



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With its potential for scalability, precision, and adaptability, nanopore sequencing is not just a tool, but it is **a platform for the future of science and global health.**



Conclusion

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It's a relatively new and developing technique: **room for innovation.**



Conclusion

The physics you study is not just a subject, but it is the foundation for technologies that can potentially make our planet healthier, cleaner, and more sustainable for generations to come.



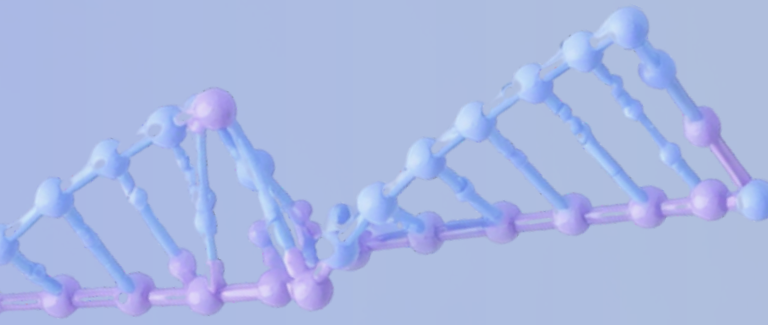


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Disclaimer: I did not receive any funding from Baci Perugina





Thank you for your attention

francesco.casadei@ausl.bologna.it
francesco.casadei20@unibo.it



Questions?

